IOWA STATE LIBRARY
DES MOINES, IOWA

THE
AMERICAN NATURALIST

VOL. LVII *July–August, 1923* No. 651

EXPERIMENTAL STUDIES ON THE DURATION OF LIFE

VIII. THE INFLUENCE UPON DURATION OF LIFE OF CERTAIN MUTANT GENES OF DROSOPHILA MELANOGASTER[1]

BIENVENIDO MARIA GONZALEZ

INTRODUCTION

IN the first part of this series Pearl and Parker (27) showed that there was a marked difference in the duration of life and in the form of the l_x curve in wild type stocks of *Drosophila* and a synthetic quintuple mutation stock. It was also pointed out in a general way that this difference was hereditary and Mendelian.

Previous to the work of Pearl and Parker (27, 32, 44, 49, 50, 61) there have been a few other studies on the duration of life of *Drosophila*. In 1911 Moenkhaus (10) made a casual reference to the fact that female flies were kept alive 153 days. In 1913 Hyde (11) in studying fertility and sterility found two strains of *Drosophila* which differed greatly in their duration of life. On breeding these he found evidence that the F_1 flies were longer lived than either parent race, and also found some indications that there was a segregation of long and short lived flies in the second filial generation (F_2). Loeb and Northrop

[1] Papers from the Department of Biometry and Vital Statistics, School of Hygiene and Public Health, Johns Hopkins University. No. 87.

Since this investigation by Dr. Gonzalez was planned and carried out as a part of the general study of duration of life going forward in this laboratory, it was thought proper to publish it in the present series. It should be said, however, that while this study forms an integral part of the work of the laboratory, Dr. Gonzalez is entirely responsible for the results and conclusions reached. Raymond Pearl.

(14–16), Northrop (17) and Lutz (13) made a number of experiments on the effects of food and temperature on the duration of life of *Drosophila*. All this early work is adequately reviewed by Pearl and Parker (*loc. cit*).

From the above papers, and the facts gathered together by Pearl (52) from the general field of biology, there seems to be little room for doubt as to the inheritance of duration of life. This fact being established, the next obvious step is to study what the factors are that control the inheritance of this character. We do know from the work of Morgan (9) and others, of numerous physical characters of an individual directly traceable to the active units of the nucleus of a cell—the chromosomes, and we know something of the behavior of these chromosomes, and the genes that are borne in them, in inheritance. But what bearing do the genes have on duration of life? Pearl, Parker and Gonzalez (57) have lately shown in great detail that in *Drosophila* duration of life is inherited in a strictly Mendelian manner. They, however, paid attention to but one morphological mutation, namely, vestigial. It is the purpose of the present paper to inquire in more detail into the influence of each of several known and established mutations upon duration of life.

MATERIAL AND METHODS

The stocks used were the Old Falmouth (wild) and the synthetic stock containing five mutants obtained from Morgan's laboratory. For convenience, the description of these two stocks as given in the first paper of Pearl and Parker is herewith reproduced:

1. Old Falmouth, Wild type fly, long bred in Morgan's laboratory. More inbred than 2 (New Falmouth).
4. Quintuple. A synthetic stock, carrying five second chromosome mutations, each in homozygous form, as follows: black, purple, vestigial, arc, and speck. Other characters wild type (Morgan). A brief description of these mutations is as follows:
   Black is a color factor affecting the body and the extremities.
   Purple is an eye color factor of the hue indicated by its name.
   Vestigial is a wing mutation in which the flies have tiny scales

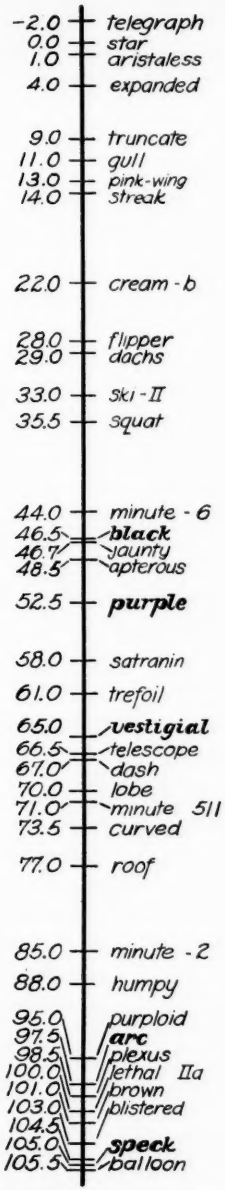


FIG. 1. Map showing the distribution of mutant loci in the second chromosome of *Drosophila melanogaster* (Oct. 15, 1920). The five mutants involved in this study are in heavier lettering.

in place of wings. The "balancers" (halteres) are similarly modified, though not to the same degree as the wings.

Arc is a wing mutation in which the wings are bent downward in an even curve, presenting a convex surface.

Speck has reference to a minute and intensely black spot in the axil of each wing.

A more detailed account and description of the above mutants may be found in Bridges and Morgan (58).

The latest map of the second chromosome as given by Bridges (59) is reproduced in Fig. 1 with the mutations used in the present study in heavier lettering.

The technique was in general the same as that described by Pearl and Parker (27). Individual matings were made with flies half a day old or younger and placed in half-pint milk bottles provided with banana agar medium. On the sixth or seventh day the parents were transferred to a second half-pint bottle. The progeny from these bottles for nine days, counting from the first day on which hatches were observed, were emptied into one ounce vials containing banana agar and these were kept separate and labeled as born on that day, and their duration of life observed. After nine days hatching the half-pint bottles were discarded. The parents have been transferred in the meanwhile into vials for observation of their duration of life also. The bottles were examined for dead flies every day, and they were changed three times during the week to give the flies fresh food. The method of handling the records was the same as that described in Pearl and Parker (27) and need not be repeated here. All these flies were kept at a constant temperature of 25° C. in an electric incubator.

Reciprocal crosses of the wild and quintuple stock were made and the F_1's mated. Cross-overs were observed and as many combinations as possible were obtained and purified. These new combinations were labeled according to their mutant phenotypic characters as follows:

00	b	(Black)
01	pr	(Purple)
02	vg	(Vestigial)
03	a	(Arc)
04	sp	(Speck)

10 bpr
11 b vg
12 b a
13 b sp
14 prvg
15 pr a
16 pr sp
17 asp

20 bpr vg
21 bpr a
22 bpr sp
23 b asp
24 pr asp
25 vg asp

30 bpr asp
31 b vgasp
32 prvgasp

The above, together with the original stocks, make a total of twenty-four different combinations of mutant genes.

Inasmuch as the character Arc is shielded when in combination with Vestigial, all Vestigial stocks were tested for the presence of Arc towards the end of the experiment. They were mated with a stock pure for Arc and containing no other mutant, and therefore dominant for Vestigial. All stocks containing Arc should give 100 per cent. Arc progeny if they are pure for this character; *vice versa,* they should show 100 per cent. straight wing (dominant to Arc) if they are pure for the absence of the character Arc. An intermediate condition shows impurity as far as the character Arc or its dominant allelomorph is concerned. Three males and three females from each bottle where progeny were obtained for the duration of life experiments were thus tested. The test revealed the following:

TABLE I

TEST OF VESTIGIAL STOCKS FOR ARC

Serial No.	Original Designation	Result of Test	New Designation
02	vg	No Arc	same
11	b vg	No Arc	same
14	prvg	No Arc	same
20	bprvg	Not pure	bprvga/
25	vgasp	Pure for Arc	same
31	b vgasp	Not pure	b vga/sp
32	prvg asp	No Arc	prvg sp
	Quintuple bprvgasp	Pure for Arc	same

This work was carried out under the direction of Dr. Raymond Pearl, from whom I received most valuable advice and encouragement. Miss Sylvia L. Parker was a constant counsellor in the details of the experimental work. Without the help of Mr. James Krucky in the preparation of media, this work could not have proceeded with the rapidity that it has. I also wish to express my indebtedness to Misses Beryl L. Reed and Mary Connor for punching my records on cards for mechanical tabulation.

FERTILITY

It was the plan to raise at least 500 individuals of each strain. For this purpose as many matings were started as were necessary to produce at least 500 flies for the duration of life experiments. Table II. shows the strains, the number of matings, the total progeny and the average progeny for nine days for the fertile matings.

TABLE II

MATINGS

Strain	No. of Fertile Matings	Progeny			Per cent Males	Average Progeny per Fertile Mating
		♂	♀	Total		
Wild	5	560	676	1236	45	247
Quintuple	18	365	420	785	46	44
b	5	335	355	690	49	138
pr	6	944	1006	1950	48	325
vg	10	245	288	533	46	53
a	7	417	470	887	47	127
sp	6	301	318	619	49	103
bpr	6	697	787	1484	47	247
b vg	5	307	388	695	44	139
b a	6	428	466	894	48	149
b sp	16	528	601	1129	47	71
prvg	10	568	523	1091	52	109
pr a	5	497	652	1149	43	230
pr sp	13	1465	1750	3215	46	247
asp	6	315	321	636	50	106
bprvga/	9	600	616	1216	49	135
bpr a	5	413	574	987	42	197
bpr sp	27	432	624	1056	41	39
b asp	17	312	270	582	54	34
pr asp	6	331	376	707	47	118
vgasp	8	287	279	566	51	71
bpr asp	26	400	576	976	41	38
b vga/sp	16	320	306	626	51	39
prvg sp	5	276	302	578	48	116
Totals	243	11343	12944	24287		

The preceding table shows at a glance the wide variability in fertility of the different strains.

The fertility value of each mutant gene, using strains containing one and two mutations[2] only, is shown in Table III.

TABLE III

FERTILITY VALUE OF MUTANTS

Strains	Total Average Progeny of Strains	Average Progeny per Strain
b, bpr, b vg, b a, b sp	744	149
pr, bpr, prvg, pr a, pr sp	1158	232
vg, b vg, prvg,	301	100
a, b a, pr a, asp	612	153
sp, b sp, pr sp, asp	527	132

Examination of the table discloses the fact that the strains having high fertility usually have purple, and those of low values almost invariably contain Vestigial. There is here a suggestion of the presence of a gene or genes determining fertility closely linked to one or more of the mutant genes studied.[3] It is hoped that at some future time a further study of this character may be made.

DURATION OF LIFE OF STRAINS CARRYING ONE MUTATION ONLY

Table IV gives the survivorship data of the five pure mutants and the original stocks.

Fig. 2 shows graphically the course taken by the l_x lines when plotted on an arithlog grid. It may be observed that neither Black nor Speck gives a survivorship curve much different from the wild parent. Purple and Arc are considerably lower than the wild stock but higher than the Quintuple. The life curve of Vestigial is the one closest to the Quintuple, though not quite as low as that.

[2] Strains involving more than two mutations would tend to mask each other's effects to a degree that would render their grouping valueless.

[3] It is at least equally probable that the true explanation of these differences in fertility associated with the presence of certain morphological mutations is the same as that for similar association of definite degrees of duration of life, set forth by Pearl, Parker and Gonzalez (57), and adopted by Gonzalez himself in the present paper *infra*.—R. P.

TABLE IV

SURVIVORSHIP DISTRIBUTION OF ORIGINAL STOCKS AND SINGLE MUTANTS (BOTH SEXES INCLUDED, NOT WEIGHTED)

Age in Days	Number of Survivors up to Indicated Age						
	Wild	Quintuple	Black	Purple	Vestigial	Arc	Speck
1	1000	1000	1000	1000	1000	1000	1000
4	998	955	991	995	996	986	985
7	992	683	987	939	938	938	977
10	971	424	974	873	809	873	963
13	948	269	970	791	664	813	932
16	901	168	949	711	527	760	900
19	882	115	928	622	394	709	884
22	858	75	890	558	306	643	855
25	831	48	854	495	206	575	827
28	799	31	832	425	150	464	792
31	743	13	768	338	105	402	745
34	705	6	690	218	62	316	687
37	592	5	619	151	43	241	643
40	519	1	503	99	30	165	614
43	424	0	420	67	8	107	544
46	342	—	371	34	2	62	468
49	247	—	293	20	0	32	417
52	194	—	241	7	—	15	333
55	117	—	196	3	—	2	273
58	88	—	119	1	—	1	207
61	67	—	65	0	—	1	149
64	45	—	30	—	—	0	102
67	32	—	20	—	—	—	50
70	20	—	14	—	—	—	24
73	8	—	3	—	—	—	15
76	1	—	1	—	—	—	2
79	0	—	0	—	—	—	2
82	—	—	—	—	—	—	0
Abs. No. of flies	1236	785	690	1950	533	887	619

Inasmuch as these mutations affect the duration of life of the two sexes differently, it is interesting to note just what are the differences in the various strains and how such variations are affected by the combination of two or more mutants in a single individual. The data in Table VI are derived from Table V.

In Black there is no significant difference in the mean duration of life of males and females, while there is in case of all other mutations. Combining Black with any of the other mutations does not alter the difference between the sexes in duration of life. In the case of Black-speck there is less difference between the duration of life of the males and females than in the case of Speck, seeming to imply that Black, while having no effect when alone

or with Purple, Vestigial or Arc, does have the effect of reducing the sex difference in Speck. This effect of Black on Speck is consistent throughout, as will be noticed later on.

Purple-speck shows no significant difference in the duration of life of males and females. Purple with Vestigial gives about the same result as Vestigial alone, indi-

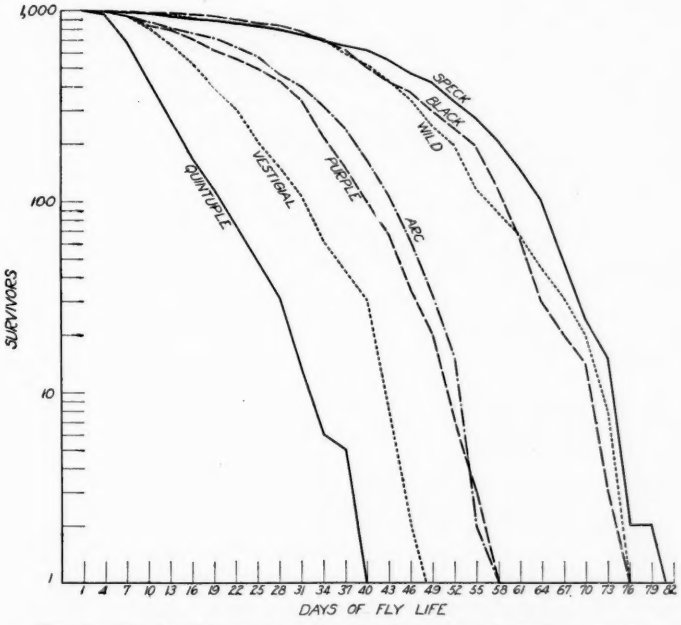


FIG. 2. Survivorship graphs of original stocks and single mutants. Both sexes.

cating that Vestigial overshadows any effects of Purple in so far as the character in question is concerned. In Purple-arc the effect of Purple is the dominant one.

In Arc-speck the result is almost the algebraic sum of the two single mutations. The greater mean duration of life is in the same direction as Speck, which has the greater value.

If we continue our observations along the same line on

the other combinations involving more than two mutants, the results are not materially different from those noted above. They are further complicated by interactions among themselves, however. For example: compare Black-purple-vestigial, not pure for Arc (♂ < ♀ 7.39), with Purple-vestigial (♂ < ♀ 7.33); Black-purple-arc (♀ < ♂ 4.50) with Purple-arc (♀ < ♂ 4.02); Black-arc-speck (♀ < ♂ 6.77) with Arc-speck (♀ < ♂ 3.72), etc.

Other instances of the evidence of the effect of single characters when all others are common to both strains in question are: Vestigial-arc-speck (♂ < ♀ 12.39) compared with Arc-speck (♀ < ♂ 3.72), Vestigial being (♂ < ♀ 6.00); Black-purple-arc-speck (♂ < ♀ .46) with Vestigial-black-purple-arc-speck (♂ < ♀ 2.67).

In other cases when the mutants involved have specific interactions among themselves, the results are not as regular. Compare Black-purple-speck (♀ < ♂ 6.77) with

TABLE V

DURATION OF LIFE OF DIFFERENT STRAINS

Strains	Mean Duration of Life			Differences between males and females ♂—♀	Difference ÷ P. E. of Diff.
	Both sexes (actual number)	Males	Females		
Wild	39.47±.28	38.08±.36	40.62±.42	— 2.54±.55	4.62
Quintuple	10.88±.16	9.45±.17	12.12±.25	— 2.67±.30	8.90
Black	40.68±.50	41.03±.53	40.33±.51	+ 0.70±.74	.95
Purple	24.54±.18	27.42±.27	21.83±.23	+ 5.59±.35	15.97
Vestigial	18.22±.29	14.98±.28	20.98±.40	— 6.00±.49	12.24
Arc	26.81±.29	25.20±.33	28.24±.37	— 3.04±.50	6.08
Speck	42.66±.47	46.63±.63	38.91±.65	+ 7.72±.91	8.48
bpr	27.35±.24	30.44±.34	24.06±.32	+ 6.38±.47	13.57
b vg	20.78±.25	16.45±.23	24.20±.40	— 7.75±.46	16.85
b a	21.71±.26	20.11±.36	23.17±.37	— 3.06±.52	5.88
b sp	31.09±.24	32.36. ±35	29.97±.31	+ 2.39±.47	5.09
prvg	15.43±.15	11.72±.13	19.05±.27	— 7.33±.30	24.43
pr a	33.71±.34	36.00±.53	31.98±.43	+ 4.02±.68	5.91
pr sp	23.30±.14	23.72±.22	22.96±.19	+ 0.76±.29	2.62
asp	36.53±.44	38.41±.58	34.69±.66	+ 3.72±.88	4.23
bpr a	32.50±.34	35.06±.55	30.56±.42	+ 4.50±.69	6.52
bpr sp	27.25±.29	31.22±.45	24.45±.37	+ 6.77±.58	11.67
b asp	30.50±.39	33.72±.53	26.80±.53	+ 6.92±.75	9.22
pr asp	39.64±.45	38.38±.62	40.67±.45	— 2.29±.77	2.97
vgasp	18.97±.37	12.81±.26	25.20±.61	—12.39±.66	18.77
prvg sp	10.62±.16	9.47±.17	12.17±.26	— 2.70±.31	8.71
bprvga/	18.53±.18	14.79±.16	22.18±.29	— 7.39±.33	22.39
b vga/sp	16.70±.25	13.97±.26	19.56±.41	— 5.59±.49	11.40
bpr asp	22.92±.28	22.65±.42	23.11±.38	— 0.46±.57	.81

TABLE VI

A COMPARISON OF THE MEAN DURATION OF LIFE OF THE TWO SEXES

Stocks	Excess in Mean Duration of Life in Days	
	Males live longer than females	Females live longer than males
Black	.70±.74	
Purple	5.59±.35	
Speck	7.72±.91	
Vestigial		6.00±.49
Arc		3.04±.50
Black-purple	6.38±.47	
Black-speck	2.39±.47	
Black-vestigial		7.75±.46
Black-arc		3.06±.52
Purple-speck	0.76±.29	
Purple-arc	4.02±.68	
Purple-vestigial		7.33±.30
Arc-speck	3.72±.88	
Black-purple speck	6.77±.58	
Black-purple-arc	4.50±.69	
Black-purple-vestigial-arc/		7.39±.33
Black-arc-speck	6.92±.75	
Purple-arc-speck		2.29±.77
Vestigial-arc-speck		12.39±.66
Purple-vestigial-speck		2.70±.31
Black-purple-arc-speck		.46±.57
Black-vestigial-arc /speck		5.59±.49
Black-purple-vestigial-arc-speck		2.67±.30

Purple-speck ($♀ < ♂$ 0.76). We have noted before this the irregular behavior of Speck combinations with either Black or Purple.

This instance of a character having a different expression in the two sexes, without involving necessarily any difference in the sex chromosomes, is not at all new. Bridges and Morgan (58) and Lynch (60) give an account of differential fertility in various mutant stocks of *Drosophila*. The females of "rudimentary" and "fused" wings in the first chromosome, "morula" and "reduced bristle" in the second, and "dwarf" in the third are infertile, while the males are fully fertile. The case is reversed in "cleft" wings of the first chromosome where the males are fertile and the females infertile.

Cases of differential fertility are by no means the rule

in the first chromosome, and such instances as have been noted above can only be conceived as being effects of the mutant genes *per se*. Then of course we have the general phenomenon of no crossing-over in the male.

Two other cases of sexual differences in the expression of a character where genes are in autosomal chromosomes have come to the notice of the writer. As these data are as yet unpublished no further mention can be made here. All we are interested in showing at present is that these sex differences in duration of life have a parallel in the literature of *Drosophila*. The basic cause of these differences may or may not be the same.

INHERITANCE OF DURATION OF LIFE IN MALES

Since sex does not affect duration of life uniformly in one direction in the different strains involved in these

TABLE VII

SURVIVORSHIP DISTRIBUTION OF MALES OF ORIGINAL STOCKS AND STRAINS INVOLVING SINGLE MUTATIONS

Age in Days	Number of Survivors up to Indicated Age						
	Wild	Quintuple	Black	Purple	Vestigial	Arc	Speck
1	1000	1000	1000	1000	1000	1000	1000
4	998	953	994	994	1000	990	990
7	998	655	991	958	922	921	987
10	984	356	976	904	727	837	980
13	968	173	976	836	563	751	960
16	937	85	961	771	384	688	934
19	912	44	943	706	273	628	924
22	879	22	896	654	184	573	897
25	854	19	863	602	73	516	877
28	821	11	839	537	24	393	854
31	757	0	764	448	8	343	824
34	716	—	678	302	0	283	784
37	541	—	606	222	—	230	751
40	429	—	504	155	—	165	728
43	327	—	427	107	—	118	651
46	223	—	367	59	—	79	571
49	129	—	290	37	—	36	525
52	105	—	248	13	—	17	415
55	71	—	218	4	—	0	332
58	59	—	131	1	—	—	262
61	50	—	78	0	—	—	196
64	39	—	45	—	—	—	136
67	29	—	27	—	—	—	76
70	20	—	24	—	—	—	37
73	12	—	3	—	—	—	20
76	2	—	3	—	—	—	0
79	0	—	0	—	—	—	—
Abs. No. of flies	560	365	335	944	245	417	301

studies, it is deemed advisable to study the two sexes separately and thus eliminate an item which will obviously complicate the interpretation of results and mask or accentuate differences through its alternating differential effect.

Table VII gives the survivorship distributions of males of the parent stocks and the five pure mutants. These figures are not very different from those in Table IV which give the survivorship distributions for whole

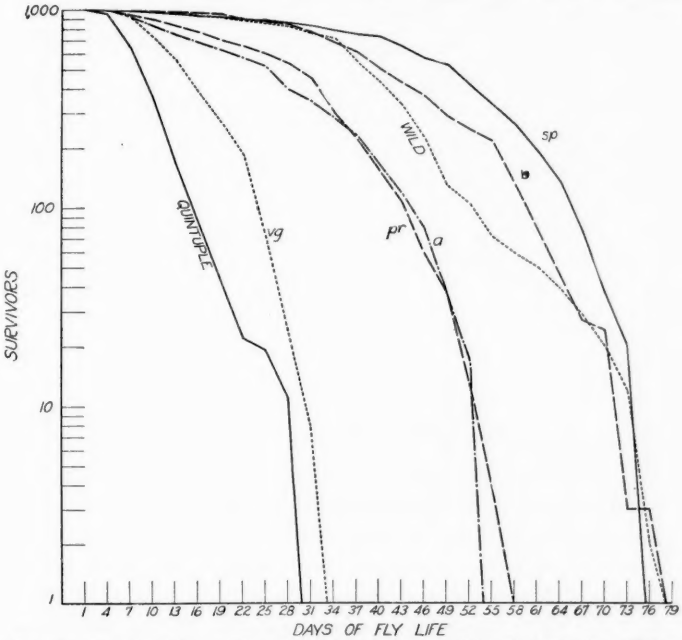


FIG. 3. Survivorship graphs of original stocks and single mutants. Males.

populations. Due to the differential effect of sex the relative position of Arc and Purple are reversed. These two characters, however, have about the same duration of life and this difference is not important. Fig. 3 shows the data in Table VII graphically. The survivorship data for the different combinations are given in Tables VIII and IX.

TABLE VIII

SURVIVORSHIP DISTRIBUTION OF MALES OF STRAINS INVOLVING TWO MUTATIONS

Age in Days	Number of Survivors up to Indicated Age							
	bpr	b vg	b a	b sp	prvg	pr a	pr sp	asp
1	1000	1000	1000	1000	1000	1000	1000	1000
4	997	993	986	996	972	992	973	994
7	971	974	907	983	901	978	924	984
10	924	876	825	962	611	944	832	968
13	887	707	724	949	336	915	745	949
16	832	472	565	922	146	871	691	911
19	768	280	463	864	67	813	623	879
22	717	163	355	763	28	748	554	822
25	656	94	276	687	11	666	463	784
28	582	55	227	617	2	610	364	746
31	492	26	180	532	0	545	282	686
34	418	7	136	470	—	485	205	600
37	336	3	100	379	—	457	151	537
40	264	0	68	282	—	412	100	495
43	184	—	30	201	—	384	61	441
46	131	—	14	159	—	338	34	371
49	75	—	12	87	—	292	24	289
52	44	—	5	61	—	217	15	216
55	19	—	2	27	—	169	12	127
58	9	—	0	8	—	135	9	67
61	6	—	—	4	—	97	4	48
64	3	—	—	2	—	64	3	29
67	1	—	—	0	—	33	2	13
70	0	—	—	—	—	0	1	3
73	—	—	—	—	—	—	1	3
76	—	—	—	—	—	—	0	3
79	—	—	—	—	—	—	—	3
82	—	—	—	—	—	—	—	3
85	—	—	—	—	—	—	—	0
Abs. No. of flies	697	307	428	528	568	497	1465	315

Examining Table X (biometric constants) we find that the mean duration of life of Black of 41.03 ± .53 days and that of Speck of 46.63 ± .63 are higher than that of the Wild stock, which is only 38.08 days. The difference between Wild and Black of 2.95 ± .64 days is not large although significant, but that between Wild and Speck, 8.55 ± .72, is very large. There is a suggestion in this of the presence of a mutant factor that increases the duration of life. Fig. 3 shows this rather clearly. Purple and Arc give a lower duration of life than the Wild stock, and Vestigial still lower.

Since we have data for so many combinations, the results are difficult to interpret *en masse*. Close observa-

TABLE IX

SURVIVORSHIP DISTRIBUTION OF MALES OF STRAINS INVOLVING THREE AND FOUR MUTATIONS

Age in Days	Number of Survivors up to Indicated Age								
	bpr a	bpr sp	b asp	pr asp	vgasp	prvg sp	bpr vga/	b vga/sp	bpr asp
1	1000	1000	1000	1000	1000	1000	1000	1000	1000
4	995	988	990	997	990	978	995	972	975
7	978	956	974	979	864	659	940	881	925
10	947	924	939	949	617	315	800	672	830
13	896	866	904	918	362	123	595	456	753
16	852	819	865	888	206	18	353	313	655
19	804	764	843	849	167	11	202	194	573
22	760	722	798	834	111	7	95	153	470
25	695	678	737	795	56	7	52	97	370
28	646	627	625	731	28	4	32	59	295
31	569	556	577	665	17	4	22	22	230
34	496	479	513	556	7	4	7	6	187
37	448	389	458	502	3	4	3	0	150
40	375	315	388	459	3	4	2	—	117
43	320	201	301	420	3	4	0	—	73
46	276	134	224	344	0	0	—	—	50
49	240	86	160	299	—	—	—	—	27
52	194	51	74	236	—	—	—	—	13
55	123	21	22	184	—	—	—	—	10
58	92	9	13	136	—	—	—	—	7
61	75	5	0	100	—	—	—	—	5
64	31	2	—	66	—	—	—	—	0
67	29	2	—	42	—	—	—	—	—
70	10	0	—	9	—	—	—	—	—
73	0	—	—	3	—	—	—	—	—
76	—	—	—	0	—	—	—	—	—
Abs. No of flies	413	432	312	331	287	276	600	320	400

tion has revealed an order which we now propose to test out. Let us assume for the moment that each of the five mutant genes studied has a definite duration of life peculiar to it, in the same manner as other genes of *Drosophila* known to control externally visible characters are, by common observation, conceded to produce flies of low or good vitality, poor in fertility or fully fertile, etc. There is the other possibility of taking duration of life as a separate character represented by a gene or genes in the chromosome, closely linked to some or all of the characters studied. As the discussion that follows will not be affected one way or the other whichever of the two views is taken, we may leave this for the present an open question.

We will first test the reaction of the different mutants with one another in respect of duration of life.

TABLE X

BIOMETRIC CONSTANTS FOR DURATION OF LIFE OF DIFFERENT STRAINS OF MALE DROSOPHILA

Strains	Number of flies	Mean (in days)	Standard Deviation (in days)	Coefficient of Variation
Wild	560	38.08±.36	12.74±.26	33.46± .75
bprvgasp Quintuple	365	9.45±.17	4.75±.12	50.26±1.63
b	335	41.03±.53	14.35±.37	34.99±1.02
pr	944	27.42±.27	12.28±.19	44.79± .82
vg	245	14.98±.28	6.41±.20	42.80±1.52
a	417	25.20±.33	9.87±.23	39.17±1.05
sp	301	46.63±.63	16.21±.45	34.76±1.06
bpr	697	30.44±.34	13.19±.24	43.32± .92
b vg	307	16.45±.23	6.09±.17	37.02±1.14
b a	428	20.11±.36	10.93±.25	54.34±1.58
b sp	528	32.36±.35	12.09±.25	37.35± .88
prvg	568	11.72±.13	4.49±.09	38.31± .87
pr a	497	36.00±.53	17.42±.37	48.40±1.25
pr sp	1465	23.72±.22	12.45±.16	52.48± .81
asp	315	38.41±.58	15.15±.41	39.44±1.21
bpr a	413	35.06±.55	16.43±.39	46.86±1.32
bpr sp	432	31.22±.45	13.73±.32	43.97±1.19
b asp	312	33.72±.53	13.75±.37	40.78±1.27
pr asp	331	38.38±.62	16.63±.44	43.32±1.33
vgasp	287	12.81±.26	6.43±.18	50.17±1.73
prvg sp	276	9.47±.17	4.30±.12	45.39±1.55
bprvga/	600	14.79±.16	5.86±.11	39.61± .88
b vga/sp	320	13.97±.26	7.02±.19	50.26±1.66
bpr asp	400	22.65±.42	12.42±.30	54.84±1.49

Combining Black with each of the others we have:

TABLE XI

Strain	Mean Duration of Life	Strain	Mean Duration of Life	Differences
Black	41.02±.53			
Purple	27.42±.27	Black-purple	30.44±.34	+ 3.02±.43
Vestigial	14.98±.28	Black-vestigial	16.45±.23	+ 1.47±.36
Arc	25.20±.33	Black-arc	20.11±.36	— 5.09±.49
Speck	43.63±.63	Black-speck	32.36±.35	—14.27±.72

From the above we can see that Black raises the value of Purple and Vestigial when it combines with them. It lowers the value of Arc and Speck. The combination

value in two cases is intermediate between that of the single mutations. In the other two cases it is lower than either component. See Figs. 4 and 5.

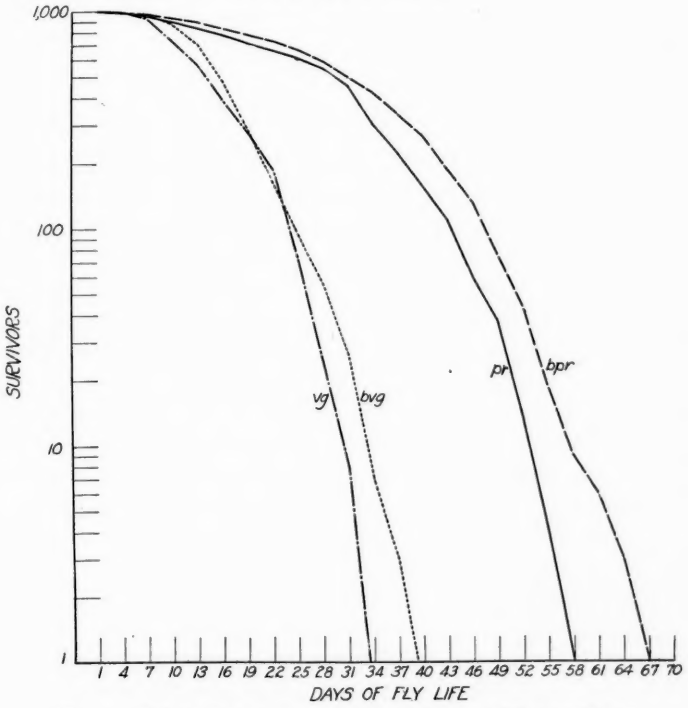


FIG. 4. Male l_x lines comparing *bpr* with *pr*, and *b vg* with *vg*.

Combining Purple with the others we have:

TABLE XII

Strain	Mean Duration of Life	Strain	Mean Duration of Life	Difference
Purple	27.42±.27			
Black	41.02±.53	Purple-black	30.44±.34	—10.58±.63
Vestigial	14.98±.28	Purple-vestigial	11.72±.13	— 3.26±.31
Arc	25.20±.33	Purple-arc	36.00±.53	+10.80±.62
Speck	46.63±.63	Purple-speck	23.72±.22	—22.91±.67

In this case Purple raised the value of Arc and lowered that of Black, Vestigial and Speck. In only a single in-

stance in the above is the combination value intermediate.

Combining Vestigial with the others we have:

TABLE XIII

Strain	Mean Duration of Life	Strain	Mean Duration of Life	Difference
Vestigial	14.98±.28			
Black	41.02±.53	Vestigial-black	16.45±.23	—24.57±.58
Purple	27.42±.27	Vestigial-purple	11.72±.13	—15.70±.30
Arc-speck	38.41±.58	Vestigial-arc-speck	12.81±.26	—25.00±.64

Vestigial-black is the only combination intermediate between that of the single mutants above. Both Vestigial-purple and Vestigial-arc-speck have lower values than their components. It was not practicable to make combinations with Arc and Speck separately, due to the masking effect of Vestigial on Arc. In every case above

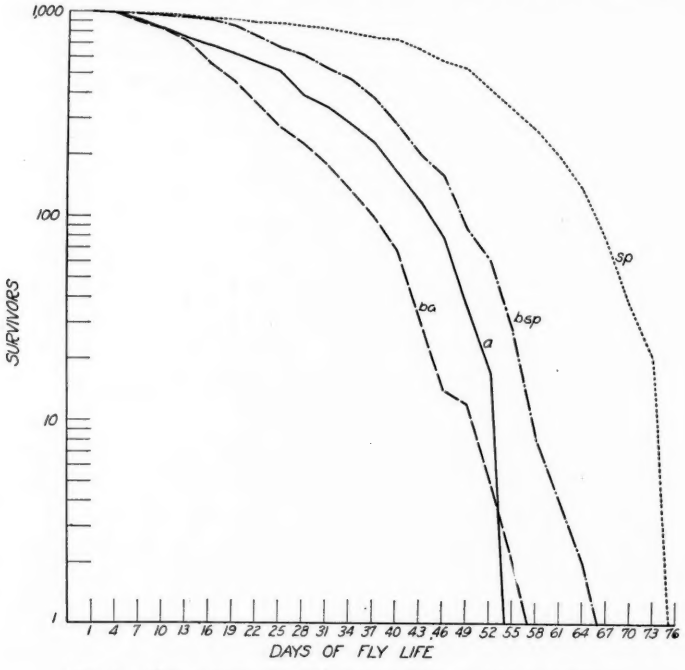


FIG. 5. Male l_x lines comparing *b sp* with *sp*, and *b a* with *a*.

Vestigial reduced the value of the other character in the combination.

From the foregoing it is evident that the duration of life of combinations is not always, nor even generally, the average of the single mutants entering in it. Also, there is interaction between different mutants which seems to be definite, if correctly understood or interpreted.

The differences noted above are all significant from the standpoint of probability. The least significant difference noted is four times its probable error (see Vestigial vs. Black-vestigial). However, since we are dealing with extremely variable material (see table of biometric constants) and in all sorts of combinations, it is best not to attach undue importance to small differences in order that we may appreciate the meaning of the larger differences.

Some facts are outstanding from the data presented above which we now propose to examine further.

1. Whenever Vestigial is at all present in a strain the value of the combination is about the same as or lower than that of Vestigial alone. This further reduction seems to be dependent on the other mutants present, Purple and Speck. Black raises the value of Vestigial to a slight extent.

TABLE XIV

Strains	Mean Duration of Life	Difference
Vestigial	*14.98±.28*	
Black-vestigial	16.45±.23	+1.47±.36
Purple-vestigial	11.72±.13	—3.26±.31
Black-purple-vestigial-arc/	14.79±.16	— .19±.32
Vestigial-arc-speck	12.81±.26	—2.17±.38
Black-vestigial-arc-speck	13.97±.26	—1.01±.38
Purple-vestigial-speck	9.47±.17	—5.51±.33
Black-purple-vestigial-arc-speck	9.45±.17	—5.53±.33

Vestigial then may be recognized as the most powerful single factor in determining duration of life among the mutants studied. It overshadows the effect of the other

characters, although its prepotency, if such we may call it, is not complete. See Figs. 6 and 7.

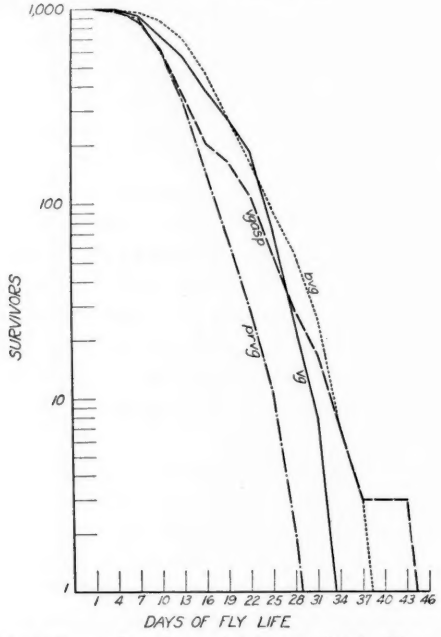


FIG. 6. Male l_x lines of stocks containing vestigial. Two mutations.

2. Whenever Vestigial is absent, Purple is the prepotent gene; that is, when present in combination with the other mutant genes, it tends either to raise or lower the value of the combination to its level. See Fig. 8.

TABLE XV

Strains	Mean Duration of Life	Difference
Purple	27.42±.27	
Black-purple	30.44±.34	+ 3.02±.43
Purple-arc	36.00±.53	+ 8.58±.60
Purple-speck	23.72±.22	— 3.70±.35
Black-purple-arc	35.06±.55	+ 7.64±.61
Black-purple-speck	31.22±.45	+ 3.80±.52
Purple-arc-speck	38.38±.62	+10.96±.68
Black-purple-arc-speck	22.65±.42	— 4.77±.50

Purple is sensibly raised by Black and Arc, especially

the latter, and lowered by Speck. The effect of Arc on Purple is a little unusual, since Arc by itself has a lower mean duration of life than Purple.

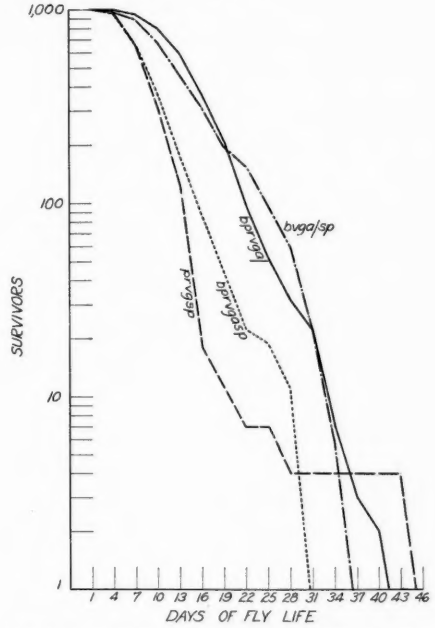


FIG. 7. Male l_x lines of stocks containing vestigial. Three or more mutants.

3. Arc is a strong modifier of the values of the other mutants. It increases the value of Purple and lowers that of Black and Speck, when taken alone.

TABLE XVI

Strains		Original Strain + Arc		Difference
pr	27.42±.27	pr a	36.00±.53	+ 8.58±.60
bpr	30.44±.34	bpr a	35.06±.55	+ 4.62±.65
pr sp	23.72±.22	pr asp	38.38±.62	+14.66±.66
vg	14.98±.28	vgasp	12.81±.26	— 2.17±.38
bpr sp	31.22±.45	bpr asp	22.65±.42	— 8.57±.61
b	41.03±.53	b a	20.11±.36	—20.92±.64
sp	46.63±.63	asp	38.41±.58	— 8.22±.86
b sp	32.36±.35	b asp	33.72±.53	+ 1.36±.64

4. Black and Speck, when alone, give flies with long duration of life, longer in fact than the Wild males. In combination the resulting strain has a lower duration of life than either component mutant. See Fig. 9. Their reaction with other mutants has already been noted in the individual discussion of such mutants.

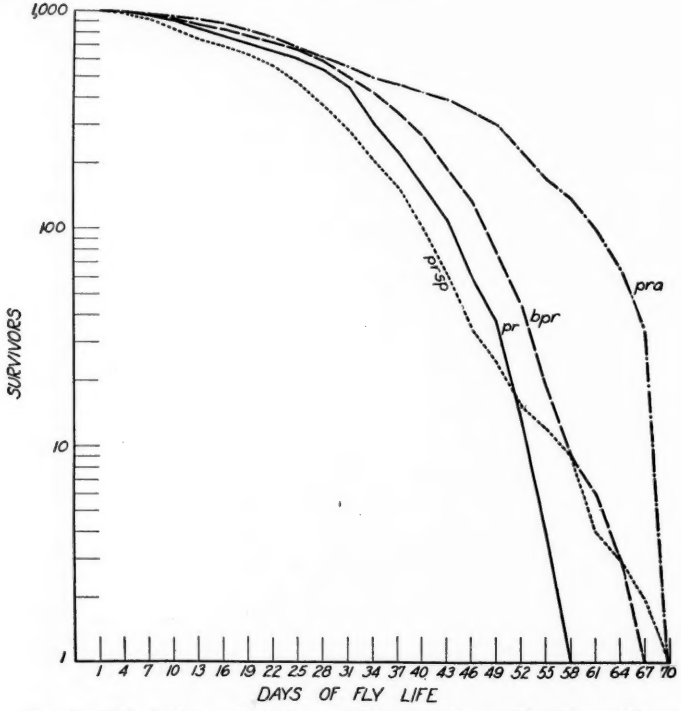


FIG. 8. Male l_x lines of stocks containing purple combinations, without vestigial.

INHERITANCE OF DURATION OF LIFE IN FEMALES

Duration of life in the females should not differ materially from that of males after due correction is made for the differences in influence of sex, if the behavior of the genes is definite in respect of duration of life. In other words, should we plot the survivorship lines of

males and females of the same strain, they should run virtually parallel to each other, maintaining a distance equal to the difference due to sex, but otherwise describing the same type of curve.

We shall test this for the five single mutants.

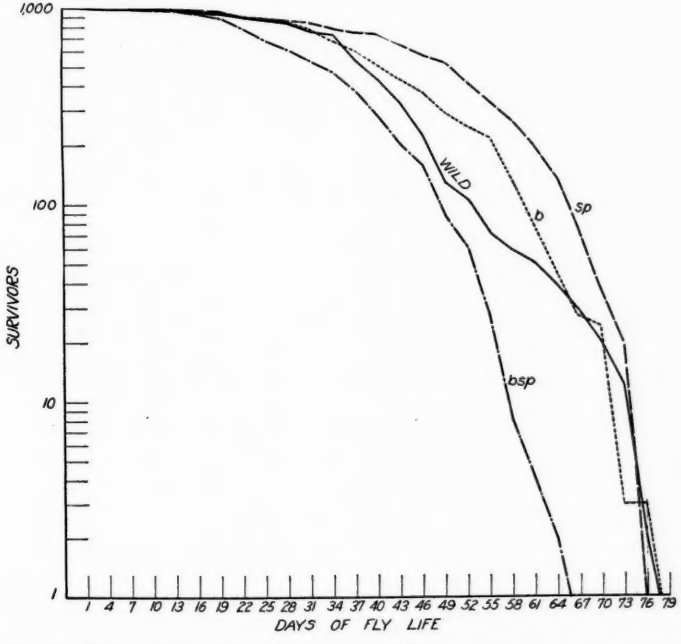


FIG. 9. Male l_x lines of *b* and *sp* compared with wild and their combination *b sp*.

Our data in Table VI show us that in:

Black—there is a non-significant difference between males and females of	$0.70 \pm .74$ days
Purple—males are longer lived by	$5.59 \pm .35$ days
Vestigial—females are longer lived by	$6.00 \pm .49$ days
Arc—females are longer lived by	$3.04 \pm .50$ days
Speck—males are longer lived by	$7.72 \pm .91$ days

Figs. 10 and 11 show that our assumption as to the effect of sex is essentially correct for Black, Purple, Vestigial and Speck. The case of Arc is a little different.

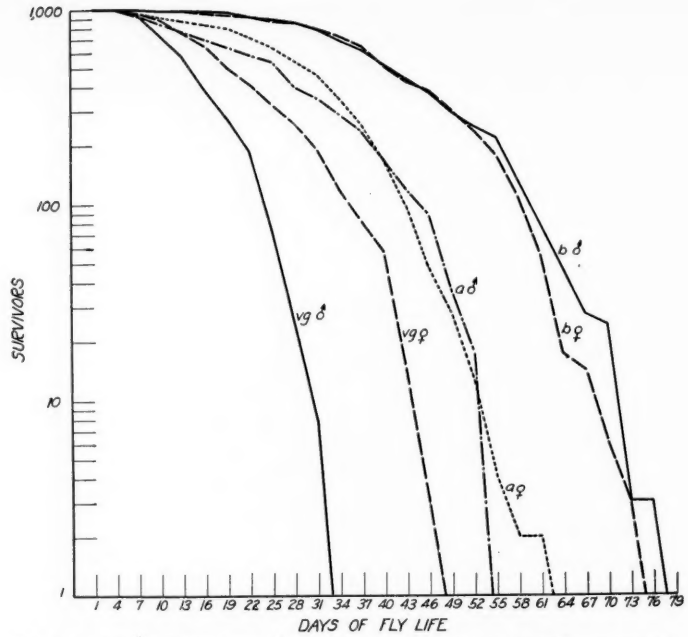


FIG. 10. Survivorship lines of *b*, *a*, and *vg*, males and females compared.

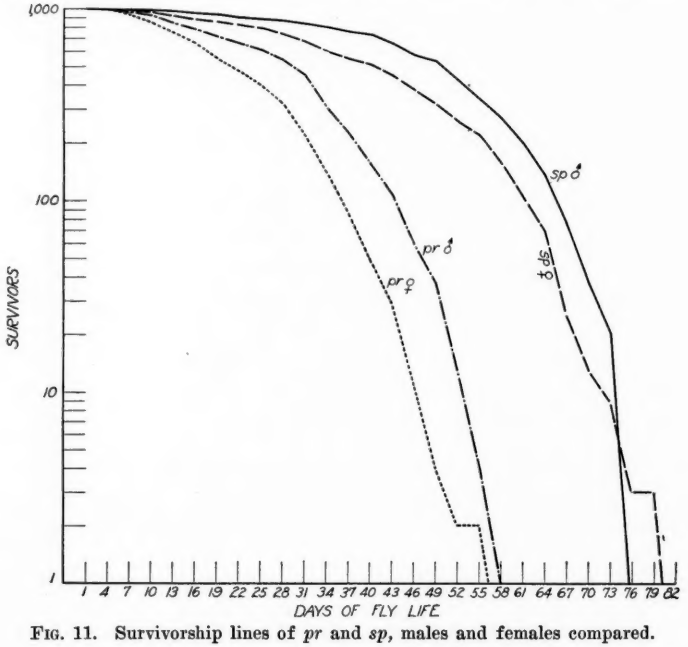


FIG. 11. Survivorship lines of *pr* and *sp*, males and females compared.

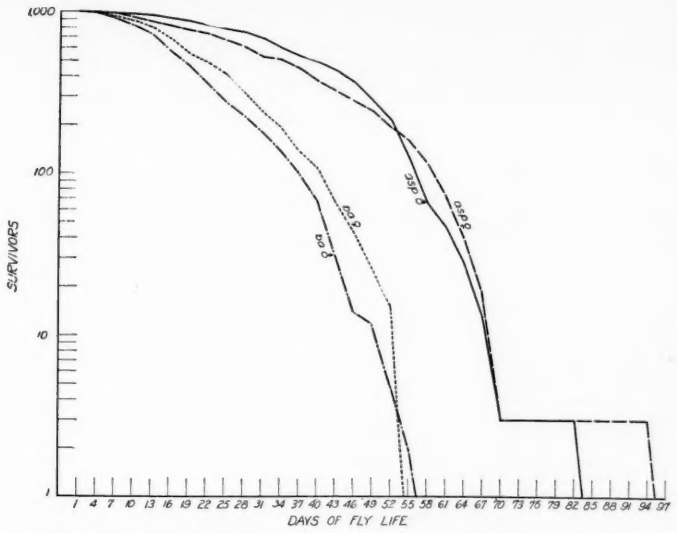


FIG. 12. Survivorship lines of Arc combinations, *b a* and *asp*, comparing male and female lines.

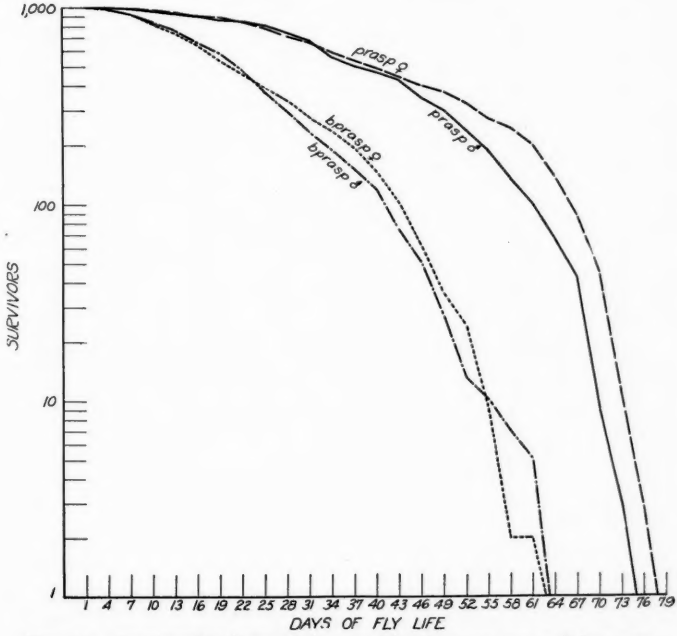


FIG. 13. Survivorship lines of Arc combinations, *pr asp* and *bpr asp*, comparing male and female lines.

In this there is a heavy mortality of males in early and later life and a low one in middle life. The case is reversed in the females, with the result that the curves cross and re-cross each other. This behavior of Arc is felt more or less in some of its combinations, as may be seen from Figs. 12 and 13, but not sufficiently to modify the general results. This characteristic of Arc, together with its property of being recessive in general yet a powerful modifier, suggests the possibility of its being a gene different in nature from the other mutations studied.

The survivorship data of the different female strains are given in Tables 17, 18 and 19, the distributions being on the basis of 1000, as in all previous tables.

TABLE XVII

SURVIVORSHIP DISTRIBUTION OF FEMALES OF ORIGINAL STOCKS AND STRAINS INVOLVING SINGLE MUTATIONS

Age in Days	Number of Survivors up to Indicated Age						
	Wild	Quintuple	Black	Purple	Vestigial	Arc	Speck
1	1000	1000	1000	1000	1000	1000	1000
4	997	957	989	996	993	983	981
7	987	707	983	921	951	953	969
10	960	483	972	844	878	904	947
13	932	352	963	749	750	868	906
16	871	240	938	655	649	823	868
19	857	176	913	543	497	781	846
22	842	121	885	468	410	704	814
25	812	74	845	395	319	628	780
28	780	48	825	319	257	528	733
31	731	24	772	235	187	455	670
34	695	12	701	139	115	345	594
37	635	10	631	84	80	251	541
40	593	2	501	48	56	164	506
43	504	0	414	29	14	98	443
46	441	—	375	11	3	47	371
49	345	—	296	4	0	28	314
52	268	—	234	2	—	13	255
55	154	—	175	2	—	4	217
58	112	—	107	0	—	2	154
61	81	—	54	—	—	2	104
64	50	—	17	—	—	0	69
67	34	—	14	—	—	—	25
70	21	—	6	—	—	—	13
73	4	—	3	—	—	—	9
76	0	—	0	—	—	—	3
79	—	—	—	—	—	—	3
82	—	—	—	—	—	—	0
Abs. No of flies	676	420	355	1006	288	470	318

TABLE XVIII

SURVIVORSHIP DISTRIBUTION OF FEMALES OF STRAINS INVOLVING TWO MUTATIONS

Age in Days	Number of Survivors up to Indicated Age							
	bpr	b vg	b a	b sp	prvg	pr a	pr sp	asp
1	1000	1000	1000	1000	1000	1000	1000	1000
4	990	982	981	992	981	1000	967	994
7	943	969	938	978	931	969	919	972
10	807	912	878	962	836	929	839	919
13	722	820	800	942	706	893	757	869
16	638	735	680	899	566	819	673	816
19	577	647	556	842	436	752	608	769
22	526	536	489	759	335	683	527	732
25	459	451	416	634	245	603	433	670
28	390	363	318	531	203	535	338	611
31	319	291	242	453	149	465	265	539
34	255	209	193	371	82	400	192	508
37	196	147	137	275	33	342	141	452
40	141	90	109	178	11	304	83	377
43	97	46	67	116	4	258	43	330
46	62	15	43	90	2	227	22	283
49	32	8	26	67	0	189	8	249
52	24	8	15	53	—	140	5	196
55	5	5	0	13	—	104	2	162
58	4	0	—	3	—	83	0	118
61	1	—	—	0	—	57	—	75
64	1	—	—	—	—	49	—	40
67	0	—	—	—	—	28	—	19
70	—	—	—	—	—	0	—	3
73	—	—	—	—	—	—	—	3
76	—	—	—	—	—	—	—	3
79	—	—	—	—	—	—	—	3
82	—	—	—	—	—	—	—	3
85	—	—	—	—	—	—	—	3
88	—	—	—	—	—	—	—	3
91	—	—	—	—	—	—	—	3
94	—	—	—	—	—	—	—	3
97	—	—	—	—	—	—	—	0
Abs. No. of flies	787	388	466	601	523	652	1750	321

TABLE XIX

SURVIVORSHIP DISTRIBUTION OF FEMALES OF STRAINS INVOLVING THREE AND FOUR MUTATIONS

Age in Days	Number of Survivors up to Indicated Age								
	bpr a	bpr sp	b asp	pr asp	vgasp	prvg sp	bprvg/a	b vga/sp	bpr asp
1	1000	1000	1000	1000	1000	1000	1000	1000	1000
4	995	966	985	997	986	974	989	974	977
7	976	910	963	992	939	801	953	886	922
10	920	833	885	963	842	540	880	804	819
13	862	732	826	928	710	354	776	693	733
16	808	655	741	902	620	189	687	562	637
19	753	595	674	875	559	126	565	454	533
22	700	532	615	832	509	83	458	363	451
25	638	486	537	774	455	56	367	288	384
28	552	401	456	702	409	36	287	206	333
31	449	346	378	649	380	33	211	160	274
34	378	264	326	582	312	17	157	108	234
37	308	215	267	527	247	10	114	82	193
40	256	152	189	487	183	3	67	52	146
43	199	95	126	434	133	0	26	26	102
46	164	54	78	396	104	—	5	16	61
49	124	40	41	367	97	—	3	10	35
52	94	22	15	322	54	—	3	3	24
55	61	11	0	269	29	—	2	0	9
58	49	3	—	242	25	—	2	—	2
61	35	2	—	199	11	—	2	—	2
64	28	2	—	138	4	—	2	—	0
67	23	0	—	88	0	—	2	—	—
70	12	—	—	45	—	—	2	—	—
73	3	—	—	11	—	—	2	—	—
76	0	—	—	3	—	—	2	—	—
79	—	—	—	0	—	—	0	—	—
Abs. No. of flies	574	624	270	376	279	302	616	306	576

The frequency constants are given in Table XX.

TABLE XX

BIOMETRIC CONSTANTS FOR DURATION OF LIFE OF DIFFERENT STRAINS OF FEMALE DROSOPHILA

Strains	Number of flies	Mean (in days)	Standard Deviation (in days)	Coefficient of Variation
Wild	676	40.62±.42	16.14±.30	39.74± .84
bprvgasp (Quintuple)	420	12.12±.25	7.50±.17	61.90±1.91
b	355	40.33±.51	14.20±.36	35.20±1.00
pr	1006	21.83±.23	10.76±.16	49.30± .90
vg	288	20.98±.40	9.95±.28	47.45±1.61
a	470	28.24±.37	11.89±.26	42.09±1.08
sp	318	38.91±.65	17.32±.46	44.52±1.41
bpr	787	24.06±.32	13.33±.23	55.39±1.20
b vg	388	24.20±.40	10.78±.26	44.56±1.28
b a	466	23.17±.37	11.80±.26	50.93±1.39
b sp	601	29.97±.31	11.44±.22	38.18± .84
prvg	523	19.05±.27	9.27±.19	48.65±1.23
pr a	652	31.98±.43	16.36±.31	51.15±1.18
pr sp	1750	22.96±.19	11.68±.13	50.89± .71
asp	321	34.69±.66	17.55±.47	50.58±1.66
bpr a	574	30.56±.42	14.99±.30	49.05±1.19
bpr sp	624	24.45±.37	13.59±.26	55.59±1.35
b asp	270	26.80±.53	12.95±.38	48.32±1.70
pr asp	376	40.67±.45	18.44±.64	45.34±1.33
vgasp	279	25.20±.61	15.11±.43	59.95±2.24
prvg sp	302	12.17±.26	6.77±.19	55.61±1.94
bprvga/	616	22.18±.29	10.64±.20	47.95±1.11
b vga/sp	306	19.56±.41	10.75±.29	54.95±1.90
bpr asp	576	23.11±.38	13.37±.27	57.85±1.49

Using the same method of examination as in males, we have:

TABLE XXI

Strains	Mean Duration of Life	Difference
Vestigial	*20.98±.40*	
Black-vestigial	24.20±.40	+3.22±.57
Purple-vestigial	19.05±.27	—1.93±.48
Black-purple-vestigial-arc/	22.18±.29	+1.20±.49
Vestigial-arc-speck	25.20±.61	+4.22±.73
Black-vestigial-arc-speck	19.56±.41	—1.42±.57
Purple-vestigial-speck	12.17±.26	—8.81±.48
Black-purple-vestigial-arc-speck	12.12±.25	—8.86±.47

The above table shows that the results with Vestigial in the female are on the whole the same as those in the

male; that is, Vestigial operates to reduce the longevity values of the mutants with which it has entered into combination to its general level. There is considerable variation, though, as its effects are modified to some extent by the other mutants, as in the case of the males. Purple and Speck tend to reduce the duration of life of the combinations further, while Black tends to raise it.

Table XXII shows the effect of Purple on the other mutants whenever Vestigial is absent.

TABLE XXII

Strains	Mean Duration of Life	Difference
Purple	*21.83±.23*	
Black-purple	24.06±.32	+ 2.23±.39
Purple-arc	31.98±.43	+10.15±.49
Purple-speck	22.96±.19	+ 1.13±.30
Black-purple-arc	30.56±.42	+ 8.73±.48
Black-purple-speck	24.45±.37	+ 2.62±.44
Purple-arc-speck	40.67±.45	+18.84±.51
Black-purple-arc-speck	23.11±.38	+ 1.28±.45

As in the males, the effect of Purple is not as pronounced as that of Vestigial, being modified considerably by the other mutations. The direction of these modifications is in the majority of cases consistent with that found in the males. Black, and especially Arc, raises its value, while Speck without a third character has little effect. See Figs. 14 and 15.

Arc also acts as a non-prepotent gene in general, in the sense that it does not bring the value of its combinations to its level, but, as in the male, it increases the value of Purple and Vestigial and lowers that of Black and Speck. The following table is illuminating on this point:

TABLE XXIII

Strain		Strain + arc		Difference
pr	21.83±.23	pr a	31.98±.43	+10.15±.49
bpr	24.06±.32	bpr a	30.56±.42	+ 6.50±.53
pr sp	22.96±.19	pr asp	40.67±.45	+17.71±.49
vg	20.98±.40	vgasp	25.20±.61	+ 4.22±.73
bpr sp	24.45±.37	bpr asp	23.11±.38	— 1.34±.53
b	40.33±.51	b a	23.17±.37	—17.16±.63
sp	38.91±.65	asp	34.69±.66	— 4.22±.93
b sp	29.97±.31	b asp	26.80±.53	— 3.17± 61

Black and Speck, individually, have as high a duration of life as the Wild stock. The two in combination give a lower duration of life than either of them alone. They together may be considered as relatively impotent, in the sense that their combinations follow the general level of duration of life of the other genes present rather than of

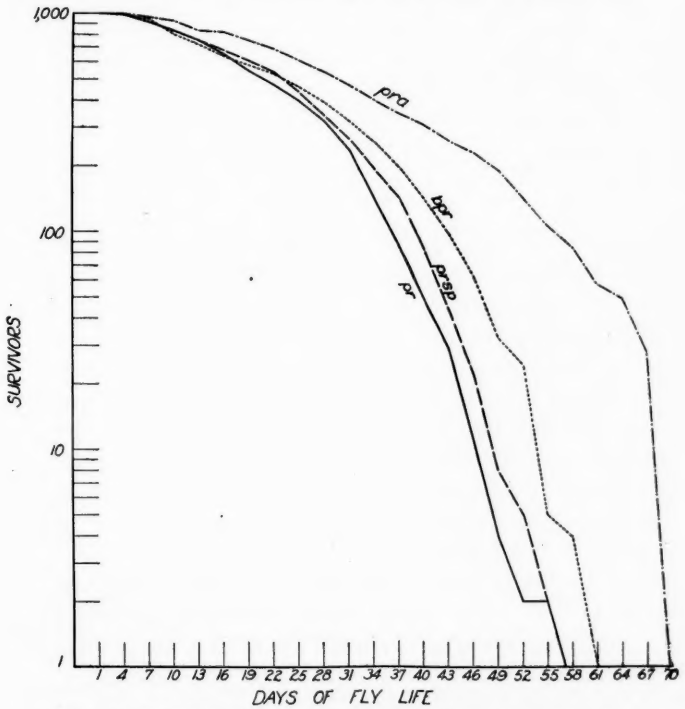


FIG. 14. Female l_x lines of purple combinations. Two mutations.

their own. When not together, however, they have a tendency to raise the duration of life of certain combinations in which they take part above that of the other mutant when alone.

DISCUSSION OF RESULTS

As a first attempt in relating duration of life to particular genes these experiments have perhaps had their

greatest usefulness in outlining future lines of endeavor, by having demonstrated that certain phenomena likely to be supposed to be concerned with duration of life have no influence over it at all. A number of theories have come to the mind of the writer during the course of these experiments, suggested mostly by the general behavior of factors already well understood. A brief mention of

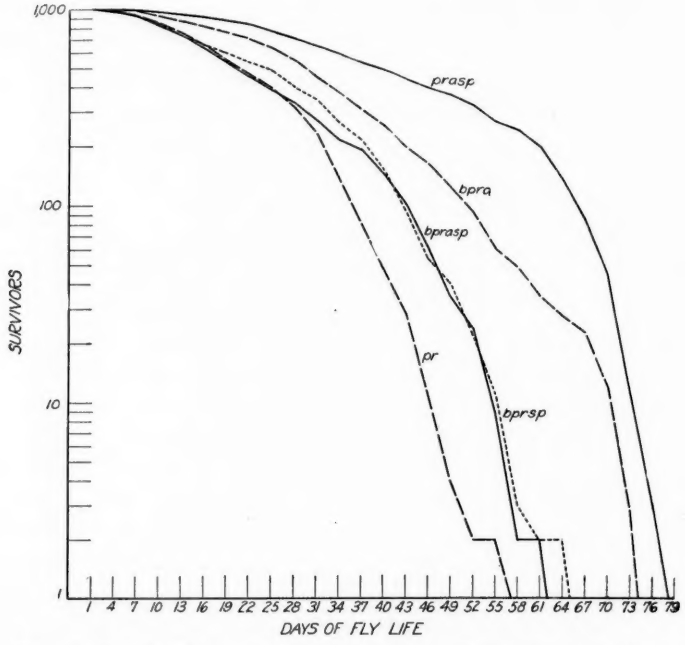


FIG. 15. Female l_x lines of purple combinations. Three or more mutations.

these will be made, as by a process of elimination of what duration of life *is not* influenced by, we may be led closer and closer to the narrower path of what *is* important in determining it.

1. *Influence of Number of "Irregular Links."* Mutations by their nature and the circumstances of their appearance may be considered as due to "abnormal" genes. If we accept Morgan's theory of linear arrange-

ment of genes, and picture the chromosomes as consisting of a string of "beads," each representing a gene, it is easy to conceive of an "abnormal bead" causing a weak link on both sides of it. If each irregular link should affect duration of life adversely, we should expect a corresponding shortening of the duration of life with the addition of each mutant gene. In other words, the number of irregular links being directly dependent on the number of these new genes, the duration of life of the resulting strain should be inversely proportional to the number of mutations it has. Our results have shown that there is no foundation for this belief, as the *number of mutant genes in a strain has no relation per se to its duration of life.*

2. *Influence of Number of Mutations.* Similarly, it is of common observation that mutants in general are not as viable, nor as fertile, nor as long lived as the wild stocks of *Drosophila.* The wild stock has been regarded as the standard, and the addition of any mutation generally lowers this standard. Sometimes it does not affect it, but I have not hitherto seen a case recorded of a mutation affecting fertility and duration of life favorably. An increase in the number of mutations in a chain might be expected to be followed by a corresponding reduction in the vital properties of the individuals. Our data show that duration of life does not primarily depend on the number of mutations in a strain, but rather on the intrinsic properties of the mutations present in it.

3. *Blending Effects of Mutant Genes.* If a number of mutant genes are known to affect duration of life definitely and yet are independent of each other, one may conceive of their behaving in this fashion: (a) The resulting combination of two or more mutants would give a duration of life which is the average of the components; or (b) if each mutant may be regarded as increasing or decreasing duration of life so many days from the standard, a combination strain would give the algebraic sum of the value of each mutation with the normal duration

of life. Neither of these alternatives is supported by the results. A good illustration is found in the case of Black and Speck. Individually they have either no effect, or increase duration of life over that of the wild strain; in combination they shorten duration of life.

4. *Physiological Effect of Mutant Genes.* Among the mutants studied Vestigial has the greatest effect on duration of life, and it so happens that it is the external character that affects most the general behavior of the fly by curtailing its normal activity. One may easily conclude that it is this physical defect, if we may regard it as so, that is the direct cause of the shortening of the duration of life of those strains containing the character Vestigial. This view has been demonstrated by Pearl *et al.* (57) to be erroneous. The duration of life of wild flies the wings of which were clipped was compared with normal ones. The results show a slightly longer duration of life in the normal ones, but not sufficient to account for the big difference between Wild and Vestigial. This small difference may properly be attributed to the injury caused to the flies in handling and clipping their young wings and in causing an open wound in the vein severed.

If further proof is necessary on this point, we have the case of Purple. This is a mutation affecting eye color, which in so far as it is possible to observe has no other effect in the physical make-up of the flies, and yet it affects duration of life to a very marked extent.

There is, therefore, a more fundamental reason for the differences in the duration of life of these mutants than any of those suggested above.

What, then, is the possible explanation?

In examining our data critically we are forced to conclude that the different mutants whose duration of life has been the object of this study behave as units in so far as this character is concerned. This behavior is as distinct and regular as the external appearance of the character which serves as an "earmark" for the identification of the gene which determines the somatic manifestation of each.

The question is whether the factors for duration of life are located in the very gene of each of the mutants studied, or whether they are separate genes, completely or very closely linked to these mutant genes. It is not probable that the five mutations picked at random as subjects for this study should, each and every one of them, be linked to a separate determiner for duration of life. We have had several years' experience in the laboratory with Vestigial stock, which contains the factor affecting duration of life most, either pure or in crosses, and involving several thousand individuals, and we have yet to find a Vestigial fly living beyond the regular span established by this character. If the gene for duration of life were a distinct and separate entity we should expect to have seen a certain proportion of long-lived Vestigial flies due to cross-overs, however small that proportion might be. The assumption, therefore, that the duration of life factors reside in the very genes of the mutants studied seems to be the more plausible and logical.

Morgan and his students have found about fifty factors that affect eye color alone. In this one study of an apparently more complicated character, in five mutants taken at random, all were found to affect duration of life. It is not too much to presume that there are many more which equally affect duration of life.

We have called attention to the fact that there is an appreciable prepotency of certain genes over others in respect of their effect upon duration of life. Such effects may be construed as of the same nature as the effects produced by the presence of a number of factors controlling the same organ but located in different parts of a chromosome or even in different chromosomes. Numerous examples are found in the mutant eye colors and wing lengths of *Drosophila.* Sometimes there is complete prepotency, as in the case of Vestigial hiding the presence of Arc absolutely; sometimes there is blending, as in the effect of Vermilion, a factor for eye color in the fifth chromosome, on Purple, another eye color factor

in the second chromosome. There are all kinds of gradations in the interaction of such factors. In our material presented above there is variety enough to overtax the descriptive words of Morgan such as "modifiers," "disproportionate modifiers," "differentiators," "sensitizers," etc.

It is a well-known fact among geneticists, especially those working with *Drosophila,* that the designation of any mutant race, White eye, for example, has reference only to that characteristic of it which is readily discernible. It is also regarded as a fact that the productivity and viability of such an individual is affected adversely as compared with the wild fly. Morgan goes a little further and states that "The productivity of the individual (of any mutant)[4] is also much affected and the viability is lower than in the wild fly." While we do not subscribe entirely to that statement, inasmuch as our data show that there is at least one mutant which actually increases duration of life, it is apparently true in more cases than it is not true. Morgan continues: "It follows that whatever it is in the germ plasm that produces white eyes also produces other modifications as well, and modifies not only such 'superficial' things as color, but also such 'fundamental' things as productivity and viability." Such being the case, the name applied to the factor is only useful in designating the conglomerate of effects which behave as a single unit in inheritance, and we may perfectly well call the separate duration of life factors recognized in these experiments "Duration of Life factor 1, 2, 3, 4 and 5," each respectively associated with visible modifications Black, Purple, Vestigial, Arc and Speck. Logically, such naming of these mutants is as sound and justifiable as to name them on the basis of morphological differences.

SUMMARY AND CONCLUSIONS

This paper is a first attempt at localizing in the chromosomes factors controlling duration of life. Five mu-

[4] The parenthetic expression is added to clarify the reference.

tants in the second chromosome of *Drosophila melanogaster* were used as indices for five distinct factors that were recognized as having definite effects on duration of life. The five mutants were contained originally in one parent strain, which, crossed with the wild stock, produced twenty-two distinct combinations. The behavior of these combinations with respect to duration of life was studied in a total of 24,287 flies.

It is shown that under constant environmental conditions, definite degrees of duration of life are associated with extreme precision and exactness with the presence or absence of certain genes in the chromosomes. These same genes also control certain morphological characters. Through the biometric treatment of the data a better insight is obtained of the interactions of factors present in different parts of the chromosome affecting the same property of the individual than has been possible with such characters as eye color and length of wing not susceptible to fine measurement.

It is also shown that some of the factors, although not sex linked, affect the sexes differently.

The above statements rest on the assumption that the units in the wild fly that are allelomorphs to the mutant genes influence or control the same characters.

LITERATURE CITED

(The plan of numbering citations is explained in the second of these Studies, AMER. NAT., Vol. 56, p. 174.)

57. Pearl, R., Parker, S. L., and Gonzalez, B. M. Experimental Studies on the Duration of Life. VII. The Mendelian Inheritance of Duration of Life in Crosses of Wild Type and Quintuple Stocks of *Drosophila melanogaster*. AMER. NAT. 1923, Vol. 57, pp. 153–192.

58. Bridges, C. B. and Morgan, T. H. The Second Chromosome Group of Mutant Characters. In "Cont. to the Genetics of *Drosophila melanogaster*." Carnegie Inst. Publ. No. 278, pp. 123–304, 1919.

59. Bridges, C. B. Current Maps of the Location of the Mutant Genes of *Drosophila melanogaster*. Proc. Nat. Acad. Sci., Vol. 7, pp. 127–132, 1921.

60. Lynch, C. J. An Analysis of Certain Cases of Intra-Specific Sterility. *Genetics*. Vol. 4, pp. 501–533.

61. Pearl, R. Experimental Studies on the Duration of Life. VI. A Comparison of the Laws of Mortality in *Drosophila* and in Man. AMER. NAT., Vol. 56, pp. 398–405, 1922.

FAMILY RESEMBLANCES AMONG AMERICAN MEN OF SCIENCE

DR. DEAN R. BRIMHALL
SECRETARY OF THE PSYCHOLOGICAL CORPORATION

IV. RESEMBLANCE AND THE DEGREE OF DISTINCTION

IT will be remembered that the starred men were arranged in an order of merit by statistical methods. In this arrangement the total number falls into four convenient groups:

These are: I. those among the leading hundred of our scientific men; II. those among the second and third hundreds; III. those below this rank in the thousand; IV. those who in the second arrangement fell below the thousand, * * *. The first three groups cover about equal ranges of merit, and this also holds in a general way for the fourth group.[1]

The positions attained are not permanent. Men advance or lose in relative position according to the merit of their performance as judged by their fellows. Whatever the variability of the position may be it seems desirable to determine the family resemblance of the different groups owing to the unique fact of the order of merit arrangement, an order that has definite objective validity.

Table XV gives the results of the comparison of the four groups according to the number with relatives of distinction.

TABLE XV

Groups	I	II	III	IV	Total
Number in each group who replied	78	174	552	152	956
Number with relatives of distinction	25	57	137	37	256
Per cent. with distinguished relatives	32.1	32.8	24.8	24.3	26.8

The two upper groups have in proportion to their numbers more among them with relatives of distinction. Aside from the first group the per cent. is progressively

[1] Cattell, *Pop. Sci. Monthly*, May, 1915.

less for the four groups. Since the positions are variable and the numbers in the different groups small it is interesting that these dissimilarities should be found. If groups one and two are combined and compared with three and four combined, the validity of the comparison should be increased; the numbers in the two groups are larger and the possibility of variability of position lessened. This arrangement makes a comparison of approximately the upper quarter with the lower three quarters. Thirty-two and five tenths per cent. of the 252 in the upper quarter and 24.7 per cent. of the lower three quarters had relatives of distinction. Seventy-six per cent. as many of the men from the lower three quarters as from the upper quarter are thus represented by relatives as defined. The validity of this ratio of 4 to 3 is not known but may be inferred from the probable errors of similar ratios in the table XVII.

Table XVI gives the comparison of the four groups in terms of the number of relatives of distinction instead of scientific men found to have such.

TABLE XVI

Groups	I	II	III	IV	Total
Number of replies	78	174	552	152	956
Number of relatives of distinction	45	105	278	70	498
Number of distinguished relatives per hundred replies	57.7	60.3	50.4	46.0	52.1

The differences have the same ranking order as those shown in table XV; the value for group one is slightly less than group two and groups three and four are progressively smaller than two or one. Compared as two groups those from the upper quarter have 59.5 and the lower three quarters 49.4 relatives per hundred men reporting. The larger group has 83 per cent. as many as the smaller or "upper quarter" group.

Table XVII gives the distribution of relatives according to the relationship and distinction of the men whose relatives they are. In this table the upper quarter is compared with the lower three quarters.

TABLE XVII

Relationship.	Number of relatives per 100 men reporting. Upper quarter.	Lower three quarters.	Per cent. values of column two in terms of column one.
Brothers and sisters	20.24	15.34	76
Sons, daughters, nieces and nephews	3.97	2.98	75
Parents	10.32	7.81	76
Uncles and aunts	7.54	6.96	92
Grandparents	6.35	5.40	85
Cousins	11.11	10.94	99
Total	59.53	49.43	83 ± 2.56

The results show an almost perfect 4–3 ratio for the three groups of near relatives and it is just those relationships that are the most significant. There is no valid difference shown in the cousin relationship. If these differences are due primarily to environmental factors, or to organic, or in part to both, it is important that we know it, but first of all it is important that we know such differences exist.

SUMMARY

The results show (1) that 32.5 per cent. of those in the upper quarter and 24.7 per cent. of those in the lower three quarters of the starred group have relatives of distinction as defined; (2) that the lower three quarters have 83 ± 2.56 per cent. as many relatives of distinction as the upper quarter.

V. THE SPECIALIZATION OF RESEMBLANCE

Table XVIII gives the distribution of relatives of men of science according to kinship and number who are distinguished for work in science. Those found only in "American Men of Science" have been omitted from this table owing to the constant error in favor of the workers in science that such inclusion would make.

TABLE XVIII

Relationship.	Total number of Distinguished Relatives.	Number of Workers in Science.	Per cent.
Brothers and sisters	140	60	43
Sons and daughters	14	12	86
Nieces and nephews	11	6	55
Parents	78	30	38
Uncles and aunts	68	16	24
Grandparents	54	13	24
Cousins	100	42	42
Total	465	179	38 ± 5.3

About 43 per cent. of the 140 comparable brothers and sisters are known for their work in science. Almost the same ratio holds for cousins. That for the parents seems to be less but it is really greater since the handbook from which most of the latter biographies come has about half the relative number of people of science that "Who's Who in America" has. The same is somewhat true for the aunts, uncles and grandparents. The number of workers in science included in Appleton's Cyclopedia was estimated by counting the number in the first five hundred. This number proved to be 37, or 7.4 per cent. of the total.

The striking resemblance in the case of the sons and daughters is probably not of valid significance owing to the small number of cases. That such resemblance should exist now when science is super-respectable is to be expected, but that it should exist in the grandparent relationship is certainly interesting, especially since 10 of the 13 grandfathers are fathers of the mothers of the men of science. Eight of the 13 are known for work in the same or closely allied sciences in which their grandsons have won renown.

Any thorough-going investigation of specialization of resemblance would require a clear definition of the function to be measured and a scale for use in measuring the amount found in any individual. There should be, say, a knowledge of what one means by astronomy and an accomplishment test by which any astronomer's work

could be measured. Obviously no such exact methods are available. We can, therefore, do no better than use these terms in the usual commonsense meaning and assume they represent somewhat similar performance. This is confessedly a rough and imperfect method and will probably become increasingly so owing to the increased overlapping of the different sciences.

No little effort was made to arrive at some method of grouping the sciences according to a classification that takes care of the overlapping. That finally adopted divides the twelve general divisions into two groups, (1) those of the more mathematical or physical sciences, (2)

TABLE XIX

DISTRIBUTION OF DISTINGUISHED RELATIVES OF MEN OF SCIENCE ACCORDING TO THE DIRECTION OF THEIR WORK AND THE DIRECTION OF THE WORK OF THE MEN WHOSE RELATIVES THEY ARE

Direction of work of distinguished relatives	Direction of Work of the Men of Science Who Have Distinguished Relatives												
	Astron.	Chem.	Geol.	Math.	Physics	Anat.	Anth.	Bot.	Path.	Physiol.	Psychol.	Zool.	Total
Astr.	4.5	1.0		.5	1.0				.3		.5		7.8
Chem.		10.0	4.5	.5	3.5		.5	1.0	2.0			4.5	26.5
Geol.		4.5	14.5	1.0	2.5				1.0	2.0	.3	2.0	27.8
Math.		1.0	1.0	3.0	1.5			.3			.5	.5	7.8
Physics	1.0	4.5	.8	1.5	18.3		1.5	2.3	3.3	.5	2.0	5.5	41.2
Anat.	1.0	4.0	1.3		.8	4.0		1.0	6.5	1.0	.5	2.3	22.4
Anth.	1.0	1.3	1.2						1.3	1.0	.5	1.8	8.1
Botany	1.0	5.5			4.0	1.0		12.0	1.5		1.5	1.0	27.5
Path.		2.8	2.3	.5	6.8			1.0	5.3	3.0	1.5	3.8	27.0
Psychol.									1.3		3.0	1.0	5.3
Zool.		2.5	1.0		3.5	1.0		3.0	1.3	.5		9.0	21.8
Art	1.0	5.0	3.0	1.0	2.0				1.5	2.0		4.0	19.5
Educ.	1.8	5.2	2.3	1.5	1.7	2.0	1.0	1.3	1.0	1.0	4.5	3.0	26.3
Physiol.					1.0		1.0			.5		.5	3.0
Invent.		.5			.3								.8
Law		13.0	4.8	1.0	10.5			2.5	6.3		3.0	6.8	47.9
Lit.	1.8	10.2	11.0	6.0	9.5		1.0	5.8	3.1	2.0	3.5	10.5	64.4
Polit.	2.4	4.5	2.3	8.5	5.3	.5		.5	.3	.5	2.0	.8	27.6
Relig.	1.0	10.7	11.4	1.0	5.8			1.3	.8	4.0	3.0	5.7	44.7
Trade	.5	5.3	2.8	1.0	3.5	.5		3.0	1.5	1.5	1.7	2.0	23.3
War		4.5	.8	1.0	.5	2.0		1.0	.7	.5		6.3	17.3
Totals	17.0	96.0	65.0	28.0	82.0	11.0	5.0	36.0	39.0	20.0	28.0	71.0	498.0

those of the biological sciences. Astronomy, chemistry, geology, mathematics and physics make up the first group and anatomy, anthropology, botany, pathology, physiology, psychology and zoology the second. It may be that the geologists are somewhat misplaced; if so, they would, it seems, be more misplaced if put with the biological sciences.

Table XIX gives the distribution of relatives according to the direction of their work and according to the work of the scientific men whose relatives they are. If a relative is known for work in two directions each is given a fractional value of one half; if in three directions each is given a value of one third.

The first column gives the distribution of 17 relatives of astronomers. Four and five tenths is the value for the number distinguished in astronomy, 1 in physics, 1 in anatomy, 1 in anthropology, 1 in botany, 1 in art and so on. The second column gives a similar distribution of 96 relatives of the chemists. The others follow in order.

The details of table XIX are given more objective form in table XX. Here, instead of the raw numbers and details within each group the per cent. values of the three groups are given in a form that makes direct comparison possible. The astronomers, for example, have

TABLE XX

PHYSICAL SCIENCES

	Astron.	Chem.	Geol.	Math.	Physics	Total
Physical sciences	32	22	32	23	33	28 ± 1.5
Biological sciences	18	17	9	2	20	14 ± 2.0
Fields other than science	50	61	59	75	47	58 ± 3.0
Total	100	100	100	100	100	100

BIOLOGICAL SCIENCES

	Anat. and Anthrop.	Bot.	Path.	Psychol.	Physiol.	Zool.	Total
Physical sciences	12	10	17	13	12	18	15 ± .7
Biological sciences	44	47	44	30	25	27	35 ± 2.4
Fields other than science	44	43	39	57	63	55	50 ± 2.4
Total	100	100	100	100	100	100	100

17 relatives, of whom 32 per cent. belong to the physical science group, 18 per cent. to the biological sciences and 50 per cent. to the group "other fields than science."

Fifty-six per cent. of the 956 men in the group belong to the physical sciences and 44 to the biological sciences. This is the distribution for the thousand and is the approximate distribution for the workers recorded in "American Men of Science." There were, therefore, at the time of the study more workers in the physical sciences than in the biological in about a 5 to 4 ratio. Instead of the ratio that might be expected as a matter of chance, namely, the 5 to 4, there is a 2 to 1 relationship with significant reliability for the relatives of the physical science group and a 3 to 7 relationship for the biological sciences. It seems incredible that these resemblances in the direction of work of a group of scientific men and their near relatives should be due to organic resemblance. However, the resemblances are there whatever the valid explanation.

Lester F. Ward, the great apostle of the doctrine of the effectiveness of environment in controlling human conduct, says:

> In certain of the arts special aptitudes are of course presupposed, and this is probably true for that great art called literature, but in the various sciences, outside of mathematics, this is not so much the case and almost any one with proper training and adequate facilities can prosecute scientific researches.[2]

A somewhat similar opinion concerning mathematics has been expressed by Cattell, as follows:

> My general opinion is that certain aptitudes, as for mathematics and music, are mainly innate, and that kinds of character and degree of ability are mainly innate, but that the direction of the performance is mainly due to the circumstances and that environment imposes a veto on any performance not congenial to it.[3]

It may be "that almost any one with proper training and adequate facilities can prosecute scientific researches," but the results of this study show that the

[2] Ward, Dynamic Psychology, p. 241.

[3] *Science*, N. S., Vol. 24, pp. 732–744.

relatives of scientific men are many times as likely to do so as men of the generality. Brothers, for example, of men of special performance in science are over 200 times as likely to show special performance in science. Moreover, near relatives are more than twice as likely to follow a dissimilar field as defined.

What of the dissimilarities? It may be that the congenital equipment which determines the performance in fields other than mathematics is also somewhat unitary, thus allowing unusual success in literature, law, education, politics, trade, science and the like. Why, for example, should the mathematicians be well represented in the field of politics, particularly diplomacy? Of their 28 distinguished relatives more are distinguished in this direction than in all the sciences; in literature they have a value of 6 and in mathematics only 3. If Galton had examined the relatives of his judges, he would no doubt have found some well known for their work in literature or politics or other fields into which their opportunities had led them. Even the men of science who are included in this study as members of the starred group are by no means limited in their special achievement to the science in question. Dean Roscoe Pound, of Harvard, is internationally known for his work as a lawyer. He is an educational administrator of recognized merit. His sister is distinguished in literature. What is one to say about the specialization of resemblance here?

I doubt if there is a family here reported in which the performance of the various individuals is not different in kind. The astronomers, for example, have three families, the Pickerings, the Searles and the Doolittles, whose work is primarily in astronomy. But, one member of the first is known for his work in ethnology and botany and one of the second is known for his work in religion. The distinguished relatives of Percival Lowell run almost the entire gamut; the brother of Ormond Stone was the head of the great Associated Press news-gathering system. Certainly these differences are as striking as the similarities that have been expressed as averages, or

as the individual cases as they stand in the lists of names. The botanists, on the other hand, have a great array of resemblances in the specific field of botany.

In discussing the number of workers in religion whose offspring became men of science, Galton says:

> Can then religion and science be in harmony? It is true that their methods are different; the religious man is attached by his heart to his religion, and can not bear to hear its truth discussed, and he fears scientific discoveries which might in some slight way discredit what he holds more important than all the rest. The scientific man seeks truth regardless of consequences * * *. These are indeed important differences, but the two characters have one powerful element in common. Neither the religious nor the scientific man will consent to sacrifice his opinions to material gain, to political ends; nor to pleasure. *Both agree in the love of intellectual pursuits* and in the practice of a simple, regular, laborious life, and both work in a disinterested way for the public good.[4]

The italics in the above quotation are the present writer's. There may be, and probably are, different kinds of intelligences. Just as there are *memories,* rather than *memory,* there are various types of intellectual performance, but these types, whatever they are, must have many elements in common. The lawyer, the minister, the educator and the man of science must respond to fine differences and shades of differences. Similarities in the finer elements of situations must be seen. The average child of three can not respond to the element or concept of "fourness." He may be able to respond by the concept "more-than-two." If he is found to respond not only to "fourness" in a group of objects of that number but to "fiveness" or "sixness" we are justified in considering him gifted in ability to do intellectual operations involving number concepts.

Professor Woodworth, in his book "Dynamic Psychology," shows how Newton recognized a similarity between the falling apple and the moon revolving about the earth. There are many persons who can not respond to this similarity with the aid of skilled teachers. So, "if the environment places a veto on any activity not con-

[4] Galton, "On the causes which operate to create scientific men," *Fortnightly Review,* Vol. XIX, pp. 345–351.

genial to it" the intellectual capacity places a veto on any environment not congenial to it. If the writer understands Professor Woodworth's argument, the mere possession of a capacity tends to its expression because the organism is "set" toward a certain activity and continues in a state of dissatisfaction until the reaction for which it is organized and prepared by original nature is in operation. Thus, if a person is so organized that he forms language habits easily and quickly he will take pleasure in forming them, if he is able to see differences in plant and animal growth, human behavior, and the like, he is ill at ease unless he is so doing and is satisfied when so doing.

If it be assumed that the performance of the individual is predicated on his congenital equipment there is still the question of how far that equipment will resemble the equipment of other individuals coming from the same or nearly related groups of germ cells. The resemblances of persons in closely related groups have been measured and shown to be many times greater than the resemblance of people chosen at random. What these resemblances mean may be left for future investigations. If society can increase its workers in science over 200 times by giving all children the same average advantages that the brothers of men of science are thought to have had, one answer is obvious. Whatever the explanation, there is no mistaking the implication that the people from the professional classes, and most of all men of science, should be given every opportunity to raise large families. The fact remains that the near relatives of these men produce far more than their share of the best that civilization offers, and it should be made easy for them to reproduce themselves, at least, until more of society can enjoy the supposed privileges enjoyed by the professional classes.

Summary

The resutls show (1) that 38 ± 5.3 per cent. of the distingiushed relatives of men of science show special per-

formance in science, which is about three times that of the distinguished people of the generality as recorded by "Who's Who in America," (2) that there is specialized resemblance in the direction of the kind of science, physical and biological—instead of the distribution of 5 relatives in the physical sciences to 4 in the biological which is the distribution in "American Men of Science," the men from the physical sciences have 2 relatives in the physical sciences to 1 in the biological, while the men of science in the biological group have 3 relatives in the physical to 7 in the biological, (3) that the dissimilarities offer perplexing data if one is to assume that resemblances are due to unitary factors of organic equipment.

VI. The Relatives of Wives of Men of Science: Assortive Mating

The two quotations given below, one from Galton and one from Ward, throw into relief an interesting question of fact. Galton claims to have been impressed with the evidence in biographical accounts of eminent men of assortive mating in the direction of intellect. He says:

> The great fact remains that able men take pleasure in the society of intelligent women, and, if they can find such as would in other respects be suitable, they will marry them in preference to mediocrities.[5]

Ward, the great proponent of the doctrine that genius is "in things" rather than men, says:

> The children of an eminent man are only half his. Half of every one of them belongs to his wife. And who is his wife? A person from entirely different stock. As geniuses are rare at best, the chances are enormously against her being a genius too. But there is a law of nature that partners choose their opposites. Galton is not ignorant of this law but he questions it.[6]

Here we have objective evidence, and to an extent in quantitative form, that Galton was correct. And who are the wives of the men of science? Of 919 of them, 57 are daughters of distinguished fathers, some of whom are world celebrities. Twenty-one of the wives are them-

[5] Hereditary Genius, 1892, p. 316.

[6] Lester F. Ward, Applied Sociology, p. 119.

selves women of distinction; 48 are sisters of men of distinction; 55 are nieces of distinguished men and 26 are granddaughters of the same sort, nor do these exhaust the relationships as table XXII shows.

Denial of assortive mating is not the only mistake of the sociologists. Ignoring it has resulted in misinterpreting apparent evidence of persistence of desirable traits coming from one individual. Consider the following in this connection:

> Remember the size, ages and financial conditions of the family when the father died—the sons being aged eight, eighteen and thirty—and then consider the fact that the three sons graduated from Princeton, and five of the daughters married college graduates, three of them Yale, and one of them Harvard and one of Princeton.[7]

The point made is that in spite of unusual obstacles three sons of the famous Jonathan Edwards graduated from college and five of the daughters showed special performance by marrying college men. It is not unlikely that the performance of the husbands of the five daughters was equal to that of the three brothers and that hereditary characters of equal value were carried by husbands and wives. Even a casual reading of the history of the Edwards family will show how a considerable portion of the stock might have been kept up by such marriages as the five original daughters made. And what of the Jukes?

The Number of Distinguished Wives

Of the 956 men concerned, 84 were reported as unmarried, 43 are known to have been married twice and two were married three times. At the time the data were gathered there had been, therefore, 919 marriages. Of these, 21 were with women of distinction as defined. Among the records of the men who did not report, 3 other wives of distinction were noted owing to cross relationship with members of the starred group. Fourteen of the 21 wives are recorded in "Who's Who in America" and 14 in "American Men of Science"; 3 of the latter

[7] Winship, Jukes-Edwards, 1900, p. 33.

being in the starred group. Fourteen are distinguished for work in science and 6 in literature.

It is not known how many of the women who are recorded in the various handbooks are married but a good many certainly are not. The number of women in "Who's Who in America" is about ten per cent. of that of the men. If every 1,000 men of the generality, belonging to the same age group as the men of science, had among them 14 distinguished wives the handbook containing their biographies would have to have nearly 200,000 accounts of married women of distinction. It is doubtful whether any volume of "Who's Who" used in this study had more than 1,000 such accounts.

DISTINGUISHED RELATIVES OF WIVES

Table XXI gives the details of the distribution of the wives and their relatives (1) according to the direction of the work of their husbands, (2) according to the number having relatives of distinction, (3) according to the number of distinguished relatives.

TABLE XXI

Direction of husband's work	(1) Total wives	Wives with distinguished relatives	Distinguished relatives
Astronomy	42	8	15
Chemistry	158	22	42
Geology	85	19	32
Mathematics	75	8	20
Physics	151	25	42
Anatomy	25	1	2
Anthropology	16	1	2
Botany	93	13	18
Pathology	53	14	31
Physiology	36	7	11
Psychology	39	4	10
Zoology	146	25	48
Total	919	147	273

The figures of table XXI show that 147, or about one in six, of the 919 women had relatives of distinction equal to that of their husbands. Sixteen of the 147 are represented only by children and as there may be some doubt

as to the validity of the comparisons which include the children when the fathers are of known distinction this number may be subtracted, making the ratio about one in seven for the number with distinguished relatives. This is more than one half as great as that of the men themselves. One hundred and thirty-one women have 254 or 1.93 relatives per individual; this is equivalent to the $1.95 \pm .06$ per individual for their husbands.

TABLE XXII

Relationship	Total	Handbooks: Am. Men of Science	Who's Who	Appleton's	Starred group
B	48	18	47	4	11
Si	10		10		
S	18	15	13		5
D	1		1		
F	57	12	35	40	10
M	3			3	
FB	28	1	4	27	
FSi	2		1	2	
MB	27	6	15	13	2
MSi					
BS	3	1	3		1
BD					
SiS	1		1		
SiD	1		1		
FF	15		1	15	
FM					
MF	11		1	10	
MM					
FBS	17	2	11	10	1
FBD	2		2		
FSiS	5	2	4		
FSiD					
MBS	14	3	10	4	3
MBD	1		1		
MSiS	9	5	7	2	4
MSiD					
Total	273	65	168	130	37

Table XXII gives the distribution of the relatives of the 147 wives (1) according to kinship, (2) according to the handbook or handbooks in which they are found reported, (3) according to the number in the starred

group. Table XXIII gives a comparison of the per cents. in each handbook and in the starred group in comparison with similar data on the husbands' relatives.

TABLE XXIII

Relatives of men of science	Am. Men of Science	Who's Who in Am.	Appleton's Cyclopedia	Starred group
498	28	62	40	11
Relatives of wives				
273	24	62	48	14

Contrary to expectation "American Men of Science" and the starred group do not have a significantly greater representation among the relatives of the men of science, that is, greater in proportion to the total number of distinguished relatives.

DISTINGUISHED BROTHERS

It is not known how comparable the brothers of the wives are with the brothers of the men of science. Assuming the two groups to be directly comparable the figures show that the brother of a wife of a man of science is about one third as likely to be known for unusual performance as a brother of a man of science. That is, 956 men of science are known to have 146 distinguished brothers; 919 of the wives have 48 such brothers. For the men of science the ratio is about 6.5 to 1; for the wives, 19.2 to 1. Since the brother of a man of science is found to be 73 times as likely as a man of the generality to be included in the handbook, "Who's Who in America," a brother of his wife would be about 24 times as likely to be included. This proportion probably errs in a negative direction. The brothers of the wives are as a group younger than the brothers of the men of science and it is likely that the data on the former group are much less complete than on the latter. Ten of the wives' sisters are distinguished and 13 of the sisters of the men of science.

OTHER RELATIVES

The relative number of distinguished parents is greater than the number of brothers. The men have 78

fathers and 3 mothers of note; the women have 57 fathers and 3 such mothers. The wives have approximately 2 fathers of distinction for 3 such fathers which the husbands have. The uncles and aunts, grandparents and cousins are represented by the numbers 68, 54, 105 for the men, and 57, 26, 48 for the wives. It is obvious that the large differences are in the remote relationships and may be accepted as evidence of greater incompleteness in the data on the relatives of the wives.

Specialization in Direction of Work

Not only are men of science likely to choose wives who on the average have more than half as many distinguished relatives as they have themselves but they are likely to choose wives whose relatives show special performance in science. Table XXIV shows the facts for the distribution of the relatives of the wives according to the degree of kinship and according to the number known for work in science. Eighty-eight, or 33 per cent., not counting those found only in "American Men of Science," of the 273 have done work in science. This compares with 38 per cent. for the same data concerning the men of science, a difference much smaller than one might expect.

TABLE XXIV

Number and Per Cent. Distinguished in Science

Relationship	Total	Number in science	Per cent. in science
Brothers and sisters	58	24	41
Sons and daughters	14	12	86
Parents	60	25	42
Uncles and aunts	56	12	21
Nephews and nieces	5	1	20
Grandparents	26	4	15
Cousins	46	10	22
Total	265	88	33 ± 5.9

The relative number of brothers in the two groups is exactly in the ratio of 1 to 1, that is, 24 in science and 24 in fields other than science; for fathers it is 1 to 1.3; for uncles, 1 to 3.8; grandparents, 1 to 6.5, and for first

cousins, male, it is 1 to 4.3. These interesting results show resemblances that increase with nearness of relationship although the different groups are not strictly comparable.

Aside from the supposition that men of intellect are attracted by women similarly gifted it is reasonable to suppose that this apparent specialization of resemblance is the result of propinquity. During the mating period sisters of colleagues or daughters of professors are likely to be companions in laboratories and social activities.

DISTINCTION AND DEGREE OF KINSHIP

Table XXV gives the distribution of the male relatives of the wives, (1) according to a coarse grouping of the number in each degree of kinship, (2) the number in each degree of kinship expressed in comparable ratio with the number in the brother relationship, (3) the same ratios expressed in the per cent. that each is of the sum of all of them.[8]

TABLE XXV

	Total	Comparable ratios	Ratios in per cents.
Brothers	48	48	33.4
Fathers	57	57	39.7
Uncles	55	27.5	19.1
Cousins	45	11.25	7.8
Total	205	143.75	100

With the exception of the brother-father relationships the results are in agreement with those found for the men of science themselves. As has been said, the brother relationship may be incomplete in that those in this degree were too young to have had time to show their performance, or owing to the mechanics of the handbooks and incompleteness of the data reported by the men or to both.

THE WIVES OF THE ZOOLOGISTS

There is a curious distribution of distinguished wives of men of science. The zoologists have 10 of the 21 who

[8] See section III for explanation of method of determination of ratios.

are included in the statistical data. The marital condition of 144 of the zoologists at the time of the investigation was as follows: 7 were unmarried, 7 had been married twice, 1 had been married three times, making 146 marriages in all. Among these 146, 10 were with women who were or later became distinguished as defined. Eight are listed as workers in zoology, 1 in psychology and 1 in literature.

This may be a chance result. The fact that the number of distinguished relatives of the wives of the zoologists is proportionately about the same as that found for each of the other sciences would seem to make it so. In any event the data are interesting in connection with the following:

> Francis Galton long ago pointed out the good results of a custom obtaining in Germany, whereby college professors tended to marry the daughters or sisters of college professors. A tendency of men of science to marry women of scientific attainments or training is marked among biologists, at least, in the United States * * *.[9]

Here we have, probably for the first time, objective evidence that zoologists tend to marry women of scientific attainments or training and that men of science, in general, tend to marry women who come from families of special intellectual performance, particularly in the direction of science.

Perhaps in the near future society will know exactly the chances of obtaining superior individuals from particular matings, assuming that it knows what superior individuals are like. It is not inconceivable that even a democracy will learn to pay a bonus for children from certain matings, trusting to the possibility of persistence of desirable traits in the same. Such a practice would facilitate the rearing and bearing of children of men and women of science if our data mean what they seem to. Now that there is evidence that men and women of science intermarry, thus increasing the chances of offspring resembling them, the suggestion of a bonus should seem less bizarre than upon first thought.

[9] Popenoe and Johnson, Applied Eugenics, 1918, p. 228.

Summary

The data in this chapter have shown (1) that a distinguished man of science is at least 200 times as likely to have a distinguished wife as a man of the generality, (2) that the direction of the performance of the wife is likely to be in science or literature, (3) excluding children, that approximately 1 in 7 of the wives has one or more relatives of distinction, which is more than half as many as the men themselves have, (4) that specialization in resemblance is shown by the fact that 33 per cent. of the distinguished relatives of the wives and 38 per cent. of the same for the men are known for their work in science, (5) that the number of distinguished relatives varies with the degree of remoteness of relationship except in the father-brother groups, (6) that the zoologists have a disproportionate share of the distinguished wives.

A LETHAL GENE IN FOWLS[1]

DR. L. C. DUNN
STORRS AGRICULTURAL EXPERIMENT STATION

SOME evidence has been secured bearing on the occurrence and inheritance of a lethal gene in fowls which appears to be closely or completely linked with a gene (c) which determines the difference between colored and recessive white plumage. Although the hypothesis offered has not been sufficiently tested, it is desired to record the present data, since the stock carrying the assumed lethal is nearly extinct and may yield no further information.

The first indications of the presence of such a gene appeared in the results obtained by crossing a Pit Game male of unknown breeding with White Wyandotte females. The F_1 generation from this cross consisted entirely of colored fowls (77). Several male offspring were crossed each with his own mother and with his full sisters, producing an F_2 generation consisting of 105 colored and 33 white (expected 103.5 : 34.5) and a backcross generation consisting of 51 colored and 29 white (equality expected). The deficiency of whites in this generation was found to be due principally to abnormal ratios in the progeny of two F_1 males. One of these males bred to his mother produced 19 colored and 8 white chicks (equality expected). By five F_1 sisters he gave a normal ratio (17 colored : 5 white). In the next season this male was bred to all his surviving relatives. Mortality in this stock was extremely high and his only surviving relatives were a daughter (colored Cc), a half sister (colored Cc) and the following white fowls: a niece, 2 aunts and 3 cousins, the latter having come from the same purebred Wyandotte stock to which his mother belonged.

[1] Contributions in Genetics No. 18, Storrs Agricultural Experiment Station.

The results of these matings were as follows:

TABLE I

RESULTS OF MATING F_1 MALE 104 (Cc) WITH VARIOUS RELATIVES

Mate	Genotype	Offspring (C) Colored	Offspring (cc) White	Offspring Total	Expected Colored	Expected White
Daughter 253	Cc	18	5	23	17.3	5.7
½ sister 44	Cc	29	5	34	25.5	8.5
Niece 199	cc	10	10	20	10.0	10.0
Total		57	20	77	52.8	24.2
Mother 8	cc	19	8	27	13.5	13.5
Aunt 12	cc	17	8	25	12.5	12.5
" 14	cc	2	1	3	1.5	1.5
[2] Cousin 505	cc	9	5	14	7.0	7.0
" 519	cc	1	2	3	1.5	1.5
" 523	cc	10	8	18	9.0	9.0
		58	32	90	45.0	45.0

In the first three matings there is a slight deficiency of whites, although not enough to require any explanation other than errors of sampling. In the matings of this male to his mother, two of her sisters and three cousins from the same pure stock, there appears a considerable departure from the expected ratio. The ratio obtained resembles a 2:1 ratio much more closely than a 1:1. In general, the white fowls are about half as numerous as should be expected if the difference between colored and white is determined by a single gene and if all combinations are equally viable.

In view of the evidence from normal ratios obtained in the F_2 generation and from other data as yet unpublished, it is certain that the white plumage of the fowls used is due to a single recessive gene. This is confirmed by the evidence and conclusions of Lippincott (1921), Sturtevant (1912) and Bateson (1902), who found what was presumably the same gene to act as a simple recessive to color. The explanation of the aberrant ratios obtained is more probably to be sought in a differential viability of the white and colored zygotes produced.

[2] Pure White Wyandottes from same stock as mother of male 104.

If we suppose (1) that a lethal gene, l, determining the death before hatching of embryos homozygous for it ll to have been introduced by female 8, the mother of male 104; (2) that this gene is closely or completely linked with c, the gene for white plumage, and (3) that this lethal gene was present in other individuals of the stock from which female 8 came, then the results obtained may be satisfactorily explained.

On the assumption that female 8 is of the genotype ccLl and male 104 is CcLl then the zygotes produced by a cross between them should be

CcLL — colored
CcLl — colored
ccLl — white (viable)
ccll — white (dies)

The resulting ratio should be 2 colored: 1 white, and the ratio of 19 colored: 8 white actually obtained agrees well with this explanation. If the other pure White Wyandotte females from the same stock were of the same genotype, *i. e.*, ccLl, then, when crossed with the male carrying the lethal, their viable offspring should be colored and white in a ratio of 2: 1. The actual ratio of all offspring from the cross of CcLl male with ccLl females contrasted with the ratio expected on the above assumptions is as follows:

	Colored	White
Actual	58	32
Expected	60	30

The numbers involved are not large, but they are thought to afford a sufficiently close agreement with the numbers expected and to support the hypothesis proposed.

It is unfortunate that more sibs of the male which was tested could not be tested thoroughly for the presence of the supposed lethal gene. Three sisters when bred to this male produced one or more white chicks while two produced no whites. On the assumption of complete linkage between c and l, no white chicks would be produced if they carried the lethal, while, if free from the lethal, colored and white chicks should be produced in

normal F_2 proportions. The numbers are not large enough to serve as a test and all sibs died before they could be mated again.

The colored daughter and half sister tested apparently did not carry the lethal since by this male they produced some white chicks. The white niece produced when bred to this male equal numbers of colored and white and probably did not carry the lethal.

In further support of the presence of the lethal may be cited: (1) An extremely high mortality of embryos early in incubation in the pure stock from which the lethal was presumably introduced (the average proportion of fertile eggs hatched in this stock was about 30 per cent.); (2) the high viability of embryos when this stock was crossed with the Pit Game, which supposedly lacked the lethal (the average proportion of fertile eggs hatched from this cross was 92 per cent.); (3) the low viability which resulted in the backcross of the lethal-bearing male to the pure Wyandotte stock (the proportion of fertile eggs hatched from this cross was about 20 per cent.). The factors responsible for mortality among embryos are too little known to place much emphasis on these latter indications; inbreeding is known to be one factor causing an increase in mortality of embryos, however, and it is probable that the segregation of lethal factors such as the one described is the primary cause of this result rather than that the inbreeding involved in producing the backcross chicks in this cross was the cause of the high mortality among embryos. (4) The mortality among the chicks hatched from crosses in which the lethal was supposedly involved was very high. It is possible that fowls heterozygous for the lethal are less viable than those which lack it entirely.

Some evidence indicates that the death of zygotes homozygous for the lethal occurs relatively early in incubation, since the ratio of colored to white chicks dying after the sixteenth day of incubation is very similar to the ratio among those actually hatched. It is hoped to

secure more evidence on this point and to test the hypothesis more fully.

REFERENCES

Bateson, W.
'02. Reports to the Evolution Committee of the Royal Society I, pp. 87–124.
Lippincott, W. A.
'21. AMERICAN NATURALIST, 45, pp. 289–327.
Sturtevant, A. H.
'12. *Journal of Experimental Zoology*, 12, pp. 499–517.

WHAT DID MAUPAS MEAN?

PROFESSOR GARY N. CALKINS
COLUMBIA UNIVERSITY

IN his fascinating little book on "Life and Death Heredity and Evolution in Unicellular Organisms," Jennings lays much stress on the conclusions which Maupas drew from his now classical experiments with isolation cultures of ciliate infusoria. Jennings uses these conclusions to support Weismann's and his own view that the primary effect of conjugation is to give rise to diverse stocks through inherited differences. In order to give effect to this interpretation he argues that in the majority of cases deterioration is probably due to faulty medium or methods and that natural death in ciliates amounts to infusoricide. "The real test lies in observing whether mating actually does remedy the degeneration. If it does not, the probability becomes strong that the degeneration is simply a pathological result of bad conditions. The evidence is becoming overwhelming that this is the case; that to avoid degeneration, it is merely necessary to avoid the bad conditions" (Jennings, 1921, p. 149). Furthermore, he holds that conjugation, except for the one case of *Uroleptus mobilis,* does not have any appreciable effect in restoring vitality as measured by the division rate, *i.e.,* it does not result in rejuvenescence.

Maupas provides ample evidence for this point of view in the two long papers which he published in 1888 and 1889, and an astute investigator would find little difficulty in digging it out. All that is needed really is patience. Jennings recognizes this and expresses it as follows: "It is because Maupas's papers, with their hundreds of pages of text filled with observational and experimental details, make hard reading, that it is possible for mistaken ideas of his results to become prevalent" (*l.c.,* p. 146). But

even the astute investigator may trip up in the tangle of inconsistencies and contradictions which these pages contain. Maupas establishes such a tangle in connection with physiological deterioration which, as he states, occurs in all of the species cultivated by him. Thus on page 266 Maupas says: "In regard to Infusoria my cultures have demonstrated experimentally that these protozoa do not escape the general law of senescence. They use themselves up and grow old by the exercise of their functions, or in other words, because of a necessity inherent in their structure and constitution. The proof that the two halves resulting from any single bipartition are equivalent is evident from all my cultures, besides it has already been furnished definitely enough by Gruber's observations on the division of testate rhizopods. But that this equivalence is continued and constantly maintained without modification from generation to generation, that an individual after 50 or 100 bipartitions, for example, would be physiologically equal to the first progenitor, this is a conclusion against which I protest. If there are actually any monoplastids (Protozoa) in which such equivalence is indefinitely maintained we know nothing of them" (*l.c.*, p. 266 and 267).

This certainly is a very explicit statement and, indeed, this is the burden of his entire experimental work in proof of advancing age and senile degeneration in infusoria. But with this conception he introduced another which is not only inconsistent but is biologically untenable, *viz.*, the idea that with this deterioration the reproductive power by division remains intact and unaltered from beginning to end of the cycle. It is this latter idea which Jennings pounces on and uses with all the skill of a trained barrister. With evident satisfaction he quotes the following passage from Maupas' paper of 1889: "I have asserted, besides, that this power of multiplication is maintained regularly and uniformly during the entire life cycle; that there is no gradual weakening of this power from the first generation after

conjugation up to the return of a new period of maturity. In other words, I deny that the infusoria after conjugation have a more energetic reproduction than they have at a later period" (p. 504). Let me add another citation from the earlier 1888 paper which adds fuel to Jennings's fire: After stating his conception of physiological usury he adds: "The power of multiplication follows no such diminishing and parallel course. It is maintained almost intact even a long time after the other functions, and the entire organism, are shown to be greatly reduced by senile degeneration. We have seen, in short, during the well-advanced stages of our cultures that the infusoria, although feeble and much reduced in size, continue to divide with almost the same rapidity as at the beginning" (1888, p. 273).

It is difficult to see how all the physiological activities of a ciliate can be gradually reduced and ultimately worn out without involving any change in the rate of multiplication by division. On this hypothesis, with loss of the powers of locomotion, food taking and digestion, growth of the daughter cells must be impaired and a next division must take place in an individual of reduced size. If this continues through 316 to 319 generations at the same division rate the ultimate products of division must be very small indeed. If physiological usury were taking place, an increasingly longer interval between successive divisions would be necessary. That such was the case in some at least of Maupas's cultures is shown by the following quotation which flatly contradicts the generalization quoted above: "In cultures begun on May 1st more than one division in twenty-four hours was no longer maintained during the months of September and October. In November and December the divisions succeeded one another at intervals of two, three and four days, and in January they were reduced to three divisions in twenty-six days" (1888, p 217). The inconsistency leads to scepticism over his results which may be expressed either in doubt as to the actual occurrence of physiological de-

terioration, or in doubt as to the invariability of the division rate.

As a matter of record Maupas hangs himself on one of the horns of the dilemma and shows by his own data that his conclusion regarding a uniform division rate for all of his cultures was incorrect. He maintained six different cultures to the end in each case, and the forms used were (1) *Stylonychia pustulata* (215 generations); (2) *Stylonychia pustulata* from an ex-conjugant (316 generations); (3) *Stylonychia mytilus* (319 generations); (4) *Onychodromus grandis* (320–330 generations); (5) *Oxytricha sp.* (320–340 generations), and (6) *Leucophrys patula* (660 generations). In at least two of these (numbers 5 and 6) the number of generations was obtained by computation on the basis of the daily temperature, a procedure which does not inspire confidence in the exactness of Maupas' methods. In connection with *Leucophrys patula* he states: "En tenant compte de la température des mois pendant lesquels cette culture a duré et de la puissance de multiplications des individus ainsi cultivées, j'ai calculé que le nombre total des générations devait attendre le chiffre de 660 au minimum au moment de l'extinction" (1888, p. 242). Again in connection with *Oxytricha sp.*: "En calculant le nombre des générations, d'apres la température des mois pendant lesquels cette culture a duré et proportionnellement a cette puissance de multiplication, j'arrive a un total approximatif de 320 à 340" (*l.c.*, p. 223).

It is unfortunate that Maupas did not see fit to publish the full records of his six cultures. Computation of divisions on the basis of the average temperature gives a result which can not be accepted, for it begs the question of decreasing vitality and multiplication. Two of his cultures must therefore be eliminated and probably a third, since he was uncertain of the length of life of *Onychodromus grandis* (320–330 generations). This leaves only three cultures from which a legitimate conclusion of an equal and continuous division rate throughout the life

cycle could be drawn. For only one of these (number 2) does he give the daily records of number of individuals, number of divisions and temperatures. "I shall not reproduce here," he says, "the daily observations of all of these species. Their detailed presentation would lead me to fastidious and uninteresting repetitions. I shall be content with giving as a specimen the longest and most complete culture which I have made. It will suffice to furnish an idea of the others" (1888, p. 196). From the various citations given above it is evident that he thought he had found that in none of his cultures was there a decrease with age, in the division rate.

It is quite evident, however, that Maupas based his generalization upon the one culture the records for which he gives in full, namely, his culture of *Stylonychia pustulata* (number 2). These records must have been constantly before him when his 1888 paper was compiled, and these must have been the only results remembered when his 1889 paper was written. They certainly bear him out. From his daily records for this culture on pages 197 to 201 it is possible to work out the average division rate for 10-day periods for the lifetime of the culture. The average temperatures for such periods can be easily computed also from the same table. These on plotting give the curve of vitality shown in Diagram 1. Making allowance for the differences in temperature it is easily seen where Maupas got the basis for his conclusion that the division rate remains practically intact from beginning to end.

Generalizations, however, are notably unsafe, particularly if they do not rest on the complete digestion of a mass of data such as Maupas must have accumulated. It is evident that he did not give equal weight to all of his records, nor is there excuse for his oversight of pertinent data which he presents in connection with another matter. He attempted to work out the approximate period in the life history of *Stylonychia mytilus* at which the micronuclei disappear. Now the disappear-

ance of the micronuclei is not a matter which interests us here, but the data used to furnish the exact age in days and generations of the individuals studied provides all the material necessary for a history of the division rate from beginning to end of the culture. This is all summarized in his 1888 paper on pages 213 and 214. The

DIAGRAM 1

Stylonychia pustulata

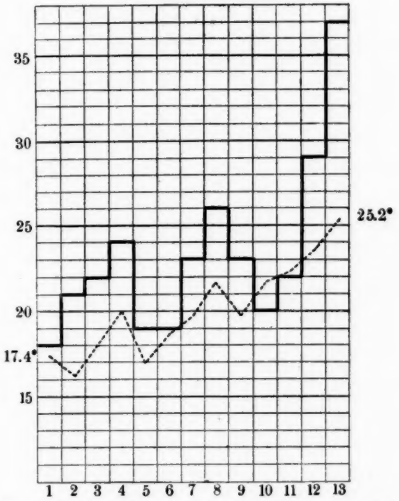


DIAGRAM 1. Generations by division of *Stylonychia pustulata* averaged for 10-day periods. From Maupas' records on pages 197–201 of his 1888 paper. The average temperatures for the same 10-day periods are shown in the dotted line curve.

culture was started on May 1, 1886, with one individual and lasted until January 26, 1887, when the last individual died in the 319th generation. The data which he thus gives us and the material for constructing a curve of vitality on the basis of 10-day division rates are condensed in the following table:

July 16 in the 148th generation (*i.e.*, 76 days from May 1st)
Aug. 15 in the 210th generation (*i.e.*, 30 days from July 16)
Sept. 14 in the 250th generation (*i.e.*, 30 days from Aug. 15)
Sept. 29 in the 261st generation (*i.e.*, 15 days from Sept. 14)

Oct. 14 in the 277th generation (*i.e.*, 15 days from Sept. 29)
Nov. 2 in the 294th generation (*i.e.*, 19 days from Oct. 14)
[1] Nov. 23 in the 305th generation (*i.e.*, 21 days from Nov. 2)
Dec. 6 in the 310th generation (*i.e.*, 13 days from Nov. 23)
Jan. 26 in the 319th generation (dead) (*i.e.*, 50 days from Dec. 6)

The full life history curve of this culture based upon the following table from these data is given in Diagram 2:

Periods	Days	Divisions	Daily Div. Rate	10-day Div. Rate	No. of 10-day Per.
From May 1 to July 16	76	= 148	1.94	19.4	7 3/5
" July 16 to Aug. 15	30	210 — 148 = 62	2.06	20.6	3
" Aug. 15 to Sep. 14	30	250 — 210 = 40	1.33	13.3	3
" Sep. 14 to Sep. 29	15	261 — 250 = 11	.73	7.3	1 1/2
" Sep. 29 to Oct. 14	15	277 — 261 = 16	1.07	10.7	1 1/2
" Oct. 14 to Nov. 2	19	294 — 277 = 17	.89	8.9	2
" Nov. 2 to Nov. 23	21	305 — 294 = 11	.52	5.2	2
" Nov. 23 to Dec. 6	13	310 — 305 = 5	.38	1.8	1
" Dec. 6 to Jan. 26	50	319 — 310 = 9	.18	3.8	5

DIAGRAM 2

Stylonychia mytilus

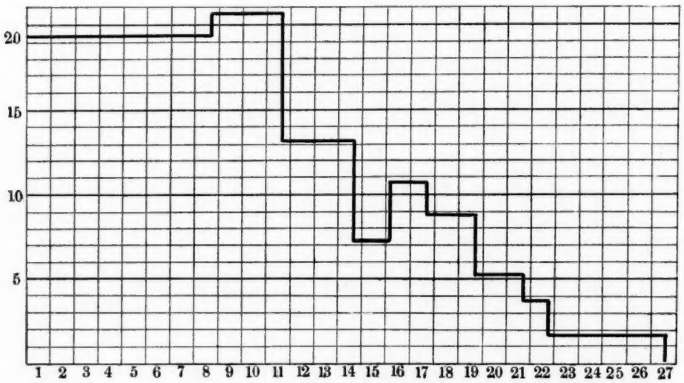


DIAGRAM 2. Generations by division of *Stylonychia mytilus* averaged for 10-day periods. From data on pages 213 and 214 of his 1888 paper.

In both diagrams the ordinates represent the number of divisions, the abscissas the consecutive 10-day periods.

[1] Maupas interpellates another date and record between November 2 and November 23 which is obviously a typographical error. After November 2 his next record is "November 28 (301st generation)," he then continues with "November 23rd (305th generation)." I have used the November 23rd record as covering and including his record labelled November 28.

This is one of three cultures of *S. mytilus,* but the only one in which he kept a daily record. All three cultures, however, "behaved in an absolutely uniform manner (Elles se sont, d'ailleurs, comportées toutes trois d'une façon absolument uniforme)" (p. 212).

Here, then, is a curve of vitality constructed from Maupas's own data which, there is no reason to doubt, are as accurate as the data for *S. pustulata.* Does this curve justify his generalization that the data for *S. pustulata* are of the same type as for all the other cultures? Does this curve justify the conclusion that the division rate remains practically the same from beginning to end? Does it support the contention that the power of multiplication is neither decreased before nor increased after conjugation? Does it give him a basis for the statement: "I deny that the infusoria after conjugation have a more energetic reproduction than they have at a later period" (1889, p. 504)? Emphatically it does not.

What did Maupas mean? The inconsistencies and contradictions have led his successors to opposite points of view. Half of Maupas's published data support one side, half support the other. Jennings is correct so far as his particular half is concerned: "Expert biologists" and "investigators as experienced as Woodruff and Erdmann" (Jennings, p. 145, footnote) were right as far as the other half was concerned. Apparently, so far as Maupas's results are to be accepted, the matter stands 50–50. This is only apparent, however, for not only does he contradict himself, but in the light of subsequent culture experiments with hypothrichous ciliates, the vitality curve for *S. pustulata* above has never been duplicated, while all later life cycles, based on better technique and more careful methods, agree with the second curve above, which we have constructed for *S. mytilus.* Thus Woodruff's (1905) curves for *Oxytricha fallax, Pleurotricha lanceolata,* and *Gastrostyla steinii* are exactly of the type which I have drawn from Maupas's data for *S. mytilus,* while the latter curve might be sub-

stituted without fear of detection, for a typical life cycle of *Uroleptus mobilis.* Indeed, the evidence is to-day overwhelming that vitality as measured by the division rate of infusoria gradually decreases with age.

Let us now consider a second point which Jennings makes in connection with the division rate subsequent to conjugation as a test of rejuvenescence. Here again his main support is derived from "that greatest of investigators of the Protozoa, Émile Maupas" (Jennings, *l.c.*, p. 64). We have given enough, however, to show what was the nature of that support. Some other experiments of Maupas bearing on this point will be mentioned later. A second great name which Jennings draws over to his own side of the argument is that of Richard Hertwig. "It is not generally realized that the work of Maupas and of Richard Hertwig, on whose authority the theories of rejuvenescence by conjugation largely rest, was squarely opposed to the idea that this rejuvenescence manifests itself by an increase of reproductive vigor. It is worth while to emphasize this point, for upon it an extraordinary error has become widespread even among expert biologists."

"Maupas rejected emphatically the idea that aging shows itself in a decrease of the rate of reproduction and that conjugation restores this declining rate. He asserted positively that no such decline occurred before conjugation and that after conjugation reproduction was not more rapid than before, and he based these statements on the results of careful experimentation. Richard Hertwig's experiments led to the same result and induced him to subscribe completely to Maupas's assertions on this point. The matter is important, since the doctrine that conjugation restores the declining fission rate depends largely on their supposed support of it" (Jennings, *l.c.*, pp. 144 and 145).

Maupas and Hertwig, therefore, should be considered together in this matter of rejuvenescence, since the theory "depends largely on their supposed support of

it." Let us first see just what Hertwig's contribution was.

In an earlier paper Jennings was not quite so happy over Hertwig's support on this problem: "He (Hertwig) gives only a general account of his experiment, not even mentioning the number of cases examined but some cultures obtained from split pairs were kept as long as three months" (Jennings, 1913, p. 358). The full extent of Hertwig's original work is expressed in the following quotation from his paper of 1889: "In order to have complete assurance on this point (division rate after conjugation) further culture records which I have had no time as yet to make, should be at hand; but I have made a very simple experiment which safely shows that conjugation-hungry infusoria maintain an intact, or as I believe, even an increased division activity, indicating a conclusion opposite to that of Bütschli and Engelmann. I have separated individuals of Paramecium which were swimming about in pairs and have cultivated them separately. For greater sureness I have separated individuals already united and within the hour of fusion and have cultivated them separately in hollow slides with nutrient media. Some of these I used in order to determine any changes during the first 24 hours but observed nothing worthy of remark; others I have maintained in culture for weeks and months. One such (*nicht einmal mit besondere Sorgfalt geführte Kultur*) lasted over three months from the end of March to the beginning of July. As a first result I noted a striking activity in divisions in animals prevented from conjugation. Although my experiments are not conclusive I may state that these artificially separated animals divide for a long time more energetically than exconjugants. In the first five days and making allowance for the period of nuclear reconstruction of the exconjugants, nearly twice as many individuals were formed" (1889, p. 222). It is hardly necessary to point out that "twice as many individuals" would mean just one more division!

The above citation includes all the experimental data and records and the sole original observations made by Hertwig, and these constitute the support which Jennings gets from him. But: "Richard Hertwig (1889) found in his experiment, to his surprise (as will any one that tries it), not only that Paramecia which had conjugated did not reproduce faster, but that, on the contrary, it was those that had not been allowed to conjugate that multiplied more rapidly" (Jennings, *l.c.*, p. 146). One swallow does not make a drink and one experiment, incomplete at that, does not give basis for a generalization. As a matter of fact, Hertwig's position in the matter was apparently based mainly on Maupas's results. His "not once with an especially carefully conducted culture" (see German above) gives his situation away. Nevertheless, Hertwig was led to say: "The grounds on which this theory is based have already been combated by Maupas; he showed by extended experiment that the power of multiplication of an infusorian is neither decreased before conjugation nor increased after it. . . . I am compelled to say that Maupas was entirely right" (quoted from Jennings, 1921, p. 147).

Let us see what further evidence, beyond the one culture of *Stylonychia pustulata* examined above, Maupas adduced in support of the conclusion that multiplication is "neither decreased before conjugation nor increased after it." On page 255 Maupas states: "I was not satisfied with this single experiment. I isolated other exconjugants of *Stylonychia pustulata,* also of *Onychodromus grandis,* of *Euplotes patella, Paramecium aurelia* and of *Leucophrys patula.* I followed, day by day, the successive generations of their descendants for periods varying from 15 days to one or two months. In none of these species have I noted the least difference in the succession of bipartitions. All of the individuals behaved in the same manner regardless of any recent or remote conjugation" (1888, p. 255). Here is another general state-

ment without accompanying data, while the scepticism raised by the discrepancy between his conclusion and his published data for the two species of Stylonychia makes one doubt the validity of this one. We are not informed as to whether his data were obtained from actual records or were computed on the basis of the temperature; also fifteen days to two months is too short a period for safe conclusions even with careful methods. In no case furthermore does he compare the division rate of the offspring with that of the parent stock for the same periods. Had he done so he would have reached a different conclusion.

Jennings apparently in 1921 is still reluctant to give up the opinion which he expressed in 1913, as follows: "But the facts appear to be clear, so far as the infusoria go. In view of the large number (*sic*) of experiments made by Maupas on this point, the absolute agreement (*sic*) of his results with those of Richard Hertwig; the fact that these men are perhaps the most thorough investigators that have ever worked along these lines; the further fact that there exist no careful experimental results opposed to these; and finally the very large body of evidence presented in the present paper, all giving the same results—is it not time that the statements or implications that in the infusoria conjugation results in increased reproduction should disappear from the literature of Science?" The fancied support which Jennings claims from these noted investigators turns out to be very questionable.

Now let us examine the evidence which Jennings himself brings to bear on the problem, evidence which, with the foregoing, he believes is enough to warrant the disappearance of further reference to rejuvenescence (increased reproduction after conjugation) in the literature of science. This evidence appears in a number of papers published by Jennings from 1908 to 1916 and is summarized in his book of 1921. The admirable thoroughness, the mastery of technique, and the skillful marshal-

ing of a wealth of data which he gives in full, together with his persuasive manner of presentation, place him immeasurably above these others whose support he claims. Indeed the only serious opponent of rejuvenescence by conjugation in ciliates is H. S. Jennings.

Unfortunately, all of Jennings's experiments, like Hertwig's, were made with, and his conclusions were drawn from one ciliate—Paramecium. Unfortunate because all conclusions as to the division rate before and after conjugation and based on experiments prior to 1914 are nullified by the discovery of monthly parthenogenesis (endomixis) made by Woodruff and Erdmann in that year. The conclusions of Hertwig (1889), of Calkins (1902–4) and of Jennings (1908–13) in regard to rejuvenescence in Paramecium are affected by this discovery, as was clearly demonstrated by Erdmann in 1919 and by Hartmann in 1921. The only exceptions allowable are those based upon observations made on the division rate in inter-endomictic periods. Of these allowable cases Jennings' paper of 1913 contains a great many, for the division rate for 11–20 days of exconjugants is contrasted with the division rate of individuals of the same age and ancestry, which were separated at the beginning of conjugation ("split" pairs). In many repeated experiments his results were uniform and his conclusion that conjugation causes a *decrease* in the division rate appears on the surface to be justified.

Another interpretation of these results, however, is possible. One result on which he laid emphasis was the invariably higher death rate and higher percentage of abnormalities of ex-conjugants as compared with non-conjugants under identical environmental conditions, a death rate amounting in one experiment to from 38 per cent. to 59 per cent. of the ex-conjugants. This he interpreted as due to "incompatible combinations" in amphimixis and as illustrating variation brought about by conjugation (1913, p. 361).

This higher death rate is significant and affects the interpretation of all of the results obtained by Jennings. Why should conjugation result in such a death rate for Paramecium when in *Uroleptus mobilis* cultivated for the last six years the death rate for ex-conjugants has been negligible, never amounting to more than three per cent.? If variation is responsible in one case there is reason to expect a like variation in the other. Variation through amphimixis is not a satisfactory explanation of the difference. Nor does it afford any explanation of the 100 per cent. of ex-conjugant mortality obtained by Bütschli with *Blepharisma lateritia;* nor of the 100 per cent. mortality obtained by Baitsell (1912) with *Stylonychia pustulata* and by Calkins (1912) with *Blepharisma undulans.* Mortality similar to that found by Jennings was also obtained by Calkins (1904) for *Paramecium caudatum.* Here the death rate of ex-conjugants from "wild" (pond) cultures amounted to from 20 per cent. to 30 per cent., but in material from prolonged laboratory cultures it rose to 94 per cent. On what basis of reasoning can we hold that incompatible combinations cause a mortality of 94 per cent. in laboratory material and only 30 per cent. in material fresh from pond water? Such cases make it very difficult to believe that variations brought about by amphimixis are responsible for the death rate. It is much more probable that appropriate environmental conditions have not been provided for the organisms during a critical period of reorganization and early development. A "standard hay infusion" was perfectly satisfactory as a culture medium for the vegetative life of *Blepharisma undulans* or for *Stylonychia pustulata,* but ex-conjugants invariably died in it. It, therefore, was an imperfect medium for these organisms, since something was lacking in it to safeguard them during a critical period. In the medium used for *Uroleptus mobilis* on the other hand, practically every ex-conjugant continues to live, if allowed to, hence it may be regarded as a per-

fect culture medium for Uroleptus. Jennings apparently takes it for granted that the standard hay infusion is the most perfect medium obtainable for Paramecium since it is suitable for the ordinary vegetative life, and he does not consider it as a possible factor in connection with the high mortality of ex-conjugants. It must be considered, however, and, in my opinion, it is a more probable cause of mortality than are "incompatible combinations."

"In Paramecium not only do those that have conjugated multiply less rapidly than before, but a great many of them die after conjugation—although without conjugation they live vigorously. Many others are weak and sickly, multiplying but little. Still further, conjugation produces a great number of abnormalities and monstrosities, such as do not occur without mating" (Jennings, 1921, p. 150). How does this bear on the fact of the decreased division rates, as found by Hertwig and Jennings for ex-conjugants? Jennings provides the application: "The grounds just set forth as possibly accounting for the greater death rate of the ex-conjugants perhaps play a part also in the production of abnormalities" (p. 361, 1913). The same causes which produce a high mortality might be expected to produce abnormalities and this would follow from reduced vitality due to imperfect cultural conditions during the critical period. Pursuing the argument a step farther, the same causes may be regarded as being responsible for the reduced division rate of ex-conjugants as compared with non-conjugants.

Certainly no such results have been obtained in my studies on *Uroleptus mobilis*. Here there is no question of the suitability of the medium, and there is an invariable increase in the division rate of the ex-conjugants over the non-conjugants. Furthermore, there is the same degree or extent of increase after conjugation in my cultures to-day as there was at the outset, and this after nearly six years of cultivation in an invariable culture medium.

In the following table each "series" represents the progeny of an ex-conjugant, the division rate of which is the average division rate of five pure lines started from the first five individuals derived from an ex-conjugant. From my 103 different series up to the present, all obtained by conjugation or by parthenogenesis from pedigreed lines, and all derived from the same single ancestral cell isolated on November 27, 1917, I have selected four groups of five successive series each, from the records for different years and chosen practically at random.

It will be noted that the extent of rejuvenescence, shown by the difference between the 60-day division rates of parent and offspring, is highly variable. It amounts to only one division per 10-days in couplet 3; to one and a half divisions in 10-days in couplets 1 and 15 but rises to a difference of 13.1 and 11.9 in couplets 7 and 14. As I have previously shown (1920), this variability is correlated with the age of the parents at the time of conjugation. Much more striking evidence of this might be selected from my records, but these are significant as random samples.

The correlation of parents' age and the extent of rejuvenescence is important in determining the significance of post-conjugation division rates. Diagram 3 shows a composite curve of vitality of the first twelve series of Uroleptus and a curve (dotted line) indicating the ideal extent of rejuvenescence in ex-conjugants at all periods. We would not attach much importance to a difference between parent and offspring of only one division in 10 days, while for a period of the first 20 days it is not an infrequent occurrence for the division rate of the offspring to fall below that of the parent. Thus in couplet number 1 the division rate of the parent for the first 20 days of the offspring's life was 19.4 per 10-days, while the rate of the offspring was 18.7; or in couplet number 3 the rate for the parent was 14.9, while that for

DIVISION RATES OF 20 COUPLETS OF OFFSPRING AND PARENTS TAKEN AT RANDOM FROM FOUR DIFFERENT YEARS OF RECORDS FOR UROLEPTUS MOBILIS

	1st 10-days	2d 10-days	3d 10-days	4th 10-days	5th 10-days	6th 10-days	Average rate 1st 60 days	Age of Parent
1 Series No. 2	18.6	18.8	16.2	16.8	17.2	15.6	17.2	
Parent No. 1	20.8	18.0	12.6	13.2	14.8	14.6	15.7	78 gen.
2 Series No. 3	16.0	18.2	16.0	17.0	17.6	18.4	17.2	
Parent No. 1	13.2	14.8	14.6	13.2	15.0	13.6	14.9	137
3 Series No. 4	13.4	13.8	16.4	19.8	20.2	19.6	17.2	
Parent No. 2	15.6	14.2	16.4	15.6	17.4	18.0	16.2	86
4 Series No. 5	17.4	19.4	21.0	19.6	15.6	15.8	18.1	
Parent B	14.4	13.8	13.6	15.0	12.2	4.0	12.1	115
5 Series No. 6	19.6	16.8	17.8	15.8	14.8	16.0	16.8	
Parent No. 1	12.8	7.4	11.0	7.0	9.0	7.6	9.1	237
6 Series No. 15	19.6	13.8	14.0	12.8	14.0	9.4	13.9	
Parent No. 8	3.6	0.8	0.2	0.4	0.2	0.0	0.8	245
7 Series No. 16	9.0	14.0	13.3	13.6	13.6	12.6	12.7	
Parent No. 9	5.4	10.0	10.4	7.6	5.6	2.6	6.9	208
8 Series No. 17	8.5	14.0	13.5	14.5	13.5	13.0	12.8	
Parent No. 9	5.4	10.0	10.4	7.6	5.6	2.6	6.9	208
9 Series No. 18	13.8	16.0	13.8	14.6	18.2	16.8	15.5	
Parent No. 13	13.6	12.8	13.2	10.0	12.4	12.2	12.3	120
10 Series No. 19	14.0	10.8	7.6	11.2	7.8	10.8	10.4	
Parent No. 11	6.6	3.0	0.6	0.0	0.0	0.0	1.7	225
11 Series No. 60	16.0	17.0	18.0	17.0	15.0	16.0	16.5	
Parent No. 59	14.4	15.6	15.2	12.6	14.6	13.6	14.3	51
12 Series No. 61	17.2	17.0	16.2	15.8	15.6	13.8	15.9	
Parent No. 59	14.6	13.6	11.8	10.4	8.6	8.4	11.2	104
13 Series No. 62	12.8	13.8	13.6	14.2	13.6	13.2	13.5	
Parent No. 60	11.0	14.0	12.8	11.6	9.4	7.8	11.1	97
14 Series No. 63	14.2	15.0	13.4	14.2	13.0	12.8	13.8	
Parent No. 56	2.6	3.4	2.8	2.2	.6	0.0	1.9	170
15 Series No. 64	15.2	15.4	14.4	11.4	12.4	13.0	13.6	
Parent No. 61	13.8	14.4	12.4	11.0	10.8	10.4	12.1	74
16 Series No. 90	13.2	15.2	17.8	15.4	14.0	16.2	15.3	
Parent No. 87	11.4	12.8	14.4	13.8	12.0	11.8	12.7	88
17 Series No. 91	12.0	16.2	17.9	14.6	16.2	16.0	15.5	
Parent No. 89	11.2	11.6	12.0	11.6	11.6	11.0	13.0	30
18 Series No. 92	17.6	14.4	13.8	13.6	19.0	17.6	16.0	
Parent No. 91	16.0	12.8	13.4	11.0	15.2	13.8	13.7	52
19 Series No. 93	17.4	14.4	15.0	12.8	18.2	17.0	15.8	
Parent No. 91	16.0	12.8	13.4	11.0	15.2	13.8	13.7	70
20 Series No. 94	13.2	11.2	10.6	16.4	15.8	14.6	13.3	
Parent No. 88	11.2	11.4	8.6	11.2	10.6	11.6	10.7	149

the offspring was only 13.6. But for the 60-day period the difference was reversed in both cases. In both of these cases the parents were in full vitality at the time of conjugation and no such approximation in rates will be found in cases where the parents were of advanced age at the time of conjugation. The age in generations of the parents at the time of conjugation is given in the last column of the table. It will be seen that as age increases the division rate of the parent does not approach at any period that of its filial series. Now if this is true for Uroleptus it may be equally true for Paramecium,

DIAGRAM 3

Uroleptus mobilis
Composite Curve of Vitality of 1st 12 Series.

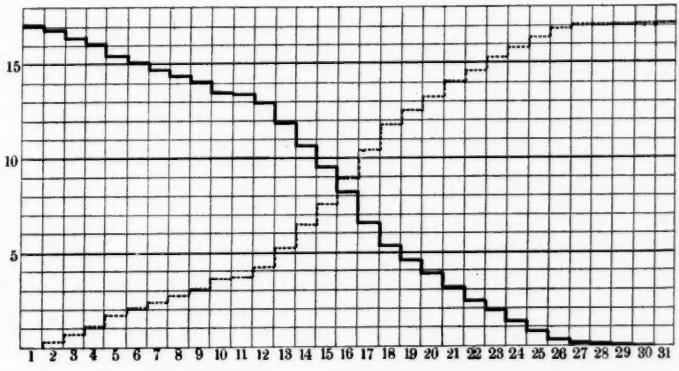


DIAGRAM 3. Composite curve of vitality of the first 12 series of *Uroleptus mobilis* by 10-day periods. The ideal expected rejuvenescence from conjugation at any period is indicated by the dotted curve.

where by virtue of the frequency of parthenogenetic periods, the parents are apparently always young. This, therefore, may be another factor to be considered in the interpretation of Jennings's results where the division rate of the offspring for a period of 21 days was sometimes less, sometimes the same as, and sometimes more than that of the parent. Because of the shortness of the

inter-endomictic period in Paramecium the vitality of parent and offspring can not be compared for more than two full 10-day periods. Neither Maupas nor Hertwig nor Jennings has furnished comparative records of parent and offspring for a longer period than 21 days.

It appears, therefore, that Jennings' recommendation to eliminate the idea of rejuvenescence from the literature of science rests on a very weak basis indeed. The support he seeks from his predecessors has failed him; the data and conclusions of Maupas are shown to be inconsistent and contradictory; those of Hertwig incomplete and inconclusive. His own experiments, so carefully planned and executed, were made on one of the most unfavorable and most unrepresentative types of organism that could have been chosen from the common ciliates. His conclusions from these experiments in respect to some of the fundamental matters in biology—rejuvenescence, heredity and variations—must remain unproved until no question can be raised as to whether culture medium, or vitality of parent, or amphimixis was responsible for the variations observed.

This criticism applies mainly to the conception of variations in vitality as adduced in proof that rejuvenescence, in the sense of increased reproduction, is not a result of conjugation. I have no quarrel with those who insist on amphimixis as a possible source of variation; the division rate indeed may be indirectly subject to such variations, but in my opinion this has never yet been proved. There is abundant evidence of variations in my records and data on *Uroleptus mobilis* which I shall analyze in the near future. One such variation is indicated in the table given above. The first quintet of couplets shows an average division rate for the first 60 days of the offspring of more than 17 divisions per 10-days for all series from young parents. The fourth quintet, made up chiefly of series from young parents, shows an average division rate of approximately only 15 divisions per 10-days for

the first 60-days. Neither this variation nor any other which I have observed shows any evidence that variations are developed in any such sudden way as Jennings maintains for Paramecium.

BIBLIOGRAPHY

Baitsell, G. A.

1912. Experiments on the reproduction of the hypotrichous Infusoria. 1. Conjugation between closely related individuals of Stylonychia pustulata. *Jour. Exp. Zool.*, Vol. 13, No. 1.

Bütschli, O.

1876. Studien über d. erst. Entwickelungsvorgan. d. Eizelle d. Zelltheilung u. die Conjugation der Infusorien. Abh. d. Senckenberg. naturforsch. Gesell. Frankfurt a/M., Bd. 10.

Calkins, G. N.

1904. Studies on the life history of Protozoa IV. Death of the A series. Conclusions. *Jour. Exp. Zool.*, Vol. 1, No. 3, p. 423.

1912. The Paedogamous Conjugation of Blepharisma undulans. *Jour. Morph.*, Vol. 23.

1919. Uroleptus mobilis Engelm II. Renewal of vitality through conjugation. *Jour. Exp. Zool.*, Vol. 29, No. 2.

1920. Uroleptus mobilis Engelm. III. A study in vitality. *Jour. Exp. Zool.*, Vol. 31, No. 2.

Erdmann, R.

1920. Endomixis and size variations in pure bred lines of Paramecium aurelia. *Arch. Entwick-Org.*, Bd. 46, Heft 1.

Hartmann, M.

1921. Untersuchungen über die Morphologie und Physiologie des Formwechsels der Phytomonadinen (Volvocales). III. Mitt. Die dauernd agame Zucht von Eudorina elegans, experimentelle Beiträge sum Befruchtungs- und Todproblem. Archiv Protist., Vol. 43, p. 223.

Hertwig, R.

1889. Ueber die Conjugation der Infusorien. Abhldg. d. II. Cl. d. königl. bayr. Akad. d. Wiss., Bd. 17, p. 151–233.

Jennings, H. S.

1913. The effect of conjugation in Paramecium. *Jour. Exp. Zool.*, Vol. 14, p. 279–391.

1921. Life and Death Heredity and Evolution in Unicellular Organisms.

Maupas, E.

1888. Recherches expérimentales sur la multiplication des infusoires ciliés. Arch. d. Zool. Exp. et Gén. (2), 6: 165–277.

1889. La rejeunissement karyogamique chez les ciliés. Arch. d. Zool. Exp. et Gén. (2), 7: 149–517.

Woodruff, L. L.

1905. An experimental study on the life history of hypotrichous Infusoria. *Jour. Exp. Zool.*, Vol. 2, No. 4, p. 585.

Woodruff, L. L., and Erdmann, R.

1914. A normal periodic reorganization process without cell fusion in Paramecium. *Jour. Exp. Zool.*, Vol. 17, p. 425–518.

SHORTER ARTICLES AND DISCUSSION

THE SUBCOSTAL VEIN IN THE WINGS OF INSECTS[1]

THE students of the wings of insects are apparently all agreed that the primitive subcosta was a two-branched vein. While there is unanimity of opinion as to the structure of this vein, there has been the greatest difference as to the way in which the two parts have been homologized or even recognized by these same students. Subcosta only rarely exists in its simplest condition, a long stem with two branches each continuing independently to and terminating in the costal margin. Such a condition is found in the wings of Hepialus, Mnemonica, Sthenopsis and Rhyacophila.

The two branches of subcosta may be modified in different ways, but whatever the line of modification there is left an unbranched vein extending from the proximal end of the wing to the margin. This unbranched vein, regardless of its origin or homology, is generally labelled as subcosta, Sc. While in the orders with accessory veins, the branches of subcosta can not be identified with certainty, yet in those wings where the accessory veins are wanting, there should be no such difficulty.

The great majority of lepidopterous wings have subcosta represented by a single unbranched vein and this vein is generally labelled as Sc. From a study of pupal and adult wings of Hepialus it has been shown that so far as this family is concerned it is always the first branch of subcosta, subcosta-one, that atrophies. The evidence for this family is conclusive whether drawn from the pupal wings, where there is a decided weakening of the tracheæ of subcosta-one, or from the adult where some individuals of the same species may have subcosta-one present in the wings of one side and wanting in the wings of the other or present in one wing of one side and wanting in the other wing of the same side. In those Hepialidæ where subcosta is unbranched, this vein is correctly labelled only as subcosta-two and never as Sc. The characteristic form and position of the subcostal vein

[1] Contributions from the Entomological Laboratories of the University of Illinois No. 76.

in the Frenatæ leaves no doubt but that this vein also should be labelled as subcosta-two. In the Lepidoptera subcosta is, therefore, modified by the atrophy of subcosta-one, and the labelling of subcosta and the subcostal cells should show this condition.

Another characteristic way in which subcosta and its branches are modified is shown by the wings of certain stone-flies, as Nemoura and Tæniopteryx. In such wings subcosta-one extends directly to the wing margin as in the primitive type while the intermediate part of subcosta-two is anastomosed with radius-one. There is a free part of subcosta-two before this anastomosis and another part beyond it which terminates in the wing-margin. This condition undoubtedly arose from the migration of subcosta-two toward radius-one until the two came into contact. There thus resulted a fusion of the two veins at one point. Since the anastomosis of subcosta-two and radius-one offers a more efficient system of bracing of the costal margin, this undoubtedly led to a continuation of the anastomosis on each side of the original point of contact, together with a straightening of the two free parts of subcosta-two, approximating closer and closer to a perpendicular condition as the anastomosis proceeded. This produced in the end the type of subcosta found in the genera of stone-flies named. This is apparently the most common way in which subcosta is modified.

The wings of stone-flies illustrate a primitive condition, but in the wings of most insects where this type of modification can be identified, the anastomosis has proceeded much farther. The proximal free part of subcosta-two, the portion connected with subcosta-one, has continued to combine with radius-one until it is an oblique or perpendicular transverse vein extending between subcosta-one and radius-one. Such a condition as this is found in the wings of the Mecoptera, Panorpa and Bittacus, and in the wings of the generalized Hymenoptera. In this latter order the parts of subcosta-one, the proximal free part of subcosta-two, the portion of subcosta-two anastomosed with radius-one, and the distal free part of subcosta-two can be readily identified in the front wings of such generalized saw-flies as those of the genera Itycorsia and Macroxyela. The hymenopterous type of subcosta, the condition found in the great majority of the species of this order, has arisen from the fusion of the stem of subcosta with that of radius, eliminating the proximal free part of subcosta-two, while subcosta-one forms a short transverse vein, cross-vein-

like, extending from the fused subcosta-two and radius. This cross-vein-like structure is found only in the saw-flies and soon disappears so that only the free part of subcosta-two is left, the short distal free portion terminating in the margin of the wing and forming the proximal end of the stigma.

A later stage in the modification of subcosta is the complete fusion of the distal free part of subcosta-two with radius-one. This is the condition characteristic of all Diptera. The simplest form of subcosta in this order is found in the wings of the Tanyderidæ, as Protoplasa and Tanyderus, and the Tipulidæ, as Limnobia, Dicranomyia, and a host of other genera. The general appearance of subcosta is only a slight change from that of the hymenopterous genera Macroxyela, Odontophyes, and Megaxyela, where the distal free part of subcosta-two is very short. The cross-vein-like proximal portion of subcosta-two, called the subcostal cross-vein by older authors, is very rarely absent in the families named. This condition has been identified by dipterologists in isolated genera of other families of Nematocerous Diptera. While subcosta-one has generally been correctly labelled in the wings of these and the free part of subcosta-two has been a few times labelled as subcosta-two, no writer on the Diptera or on the wings of insects has given the vein behind subcosta-one its proper designation, subcosta-two plus radius-one. The subcostal part of the label has always been ignored. The wings of the species of Conops, a genus widely separated from all those just named, has a cross-vein-like structure located near the tip of subcosta-one. A similar condition is found in the wings of Zodion and Stylogaster, other genera of Conopidæ. That such widely separated genera should have similar structures in the subcostal region has excited my interest for several years. No one apparently has mistrusted, judging at least from published results, that any of the intervening genera between Conops and the Tipulidæ had retained any indication of the cross-vein-like proximal transverse part of subcosta-two. Instead of its being the exception that this free part of subcosta-two is preserved, it is in reality more exceptional to find this vein wanting. It is the rule, therefore, to have subcosta branched in the Diptera and not a single vein.

The subcostal fold and the migration of the free part of subcosta-two far toward the proximal end of the wing, together with the fact that no one apparently has looked for it, accounts for

the free part of subcosta-two not having been found. This vein may occur anywhere between the tip of subcosta-one and the humeral cross-vein, frequently nearer the cross-vein and often in line with it. There is for instance a distinct free part of subcosta-two in Midas, Hilaria, Docosia, Tabanus, Rhyphus, Hesperinus, Culex, Dixa, Leptis, Erax and Calliphora. The transverse thickening in the stem of radius opposite the humeral cross-vein should not be mistaken for subcosta-two.

The proximal portion of subcosta is not as a rule fused with radius as most of the drawings of dipterous wings would indicate. The subcosta is always folded under the radial stem, and when wings are examined from above as those mounted on slides, the base of the subcosta is concealed. It would not be strange, therefore, that in specialized wings there should be a fusion of these two closely placed veins. Such a condition has been developed for instance in Scenopinus, Eristalis, Eulonchus, and Calliphora. This fusion extends distal to the region of the humeral cross-vein. The free part of subcosta-two has apparently been merged with this fusion, for in most wings it can not be identified where the fusion exists. Calliphora is an exception. In the wings of this genus the stems of subcosta and radius are fused and the free part of subcosta-two is retained, but is located near the fusion. This condition supports the contention that the free part of subcosta-two is lost through its combination with this fusion. The evidence is conclusive that in all dipterous wings, the single vein in front of radius should always be labelled as subcosta-one, never as Sc, and that the next vein should always be labelled as subcosta-two plus radius-one, regardless of the fact as to whether the proximal free part of subcosta-two is present or not; if wanting it has either fused with the fused stems of radius and subcosta or has atrophied.

ALEX. D. MACGILLIVRAY

UNIVERSITY OF ILLINOIS

INHERITANCE OF MESOCOTYL LENGTH IN HYBRIDS OF BRACHYTIC MAIZE

EXPERIENCE has shown that deep planting often is desirable with maize if good stands are to be obtained under semi-arid conditions. Most commercial varieties are not adapted for deep planting and the indications are that even in the corn-growing sections the young seedlings frequently are handicapped through

planting the seeds below their optimum depth. The depth below which seeds should not be planted is indicated by the length of the mesocotyl, the organ which enables the young seedling to reach the surface.[1]

In considering the utilization of the drought-resistant possibilities of brachytic maize plants the problem of deep planting was encountered, for if full advantage were to be taken of the brachytic characters it was necessary to combine with them the feature of deep planting.

The brachytic variation arose in a hybrid having the Chinese waxy type as one parent.[2] This type of maize, adapted to the low flood plains of the Yangtze, has the shortest mesocotyl as yet found and in consequence requires very shallow planting. It became of interest, therefore, to determine whether this disadvantage, from the standpoint of drought resistance, could be overcome through hybridization with strains not handicapped with short mesocotyls.

Hybrids were made with the Hopi type of maize which Collins had found could be planted 18 cm below the surface, some plants even having mesocotyls 36 cm long. Since the brachytic variation is characterized by shortened internodes, which follow rather definite Mendelian inheritance, and since the mesocotyl is interpreted generally as an internode little success was to be expected in attempting to combine, through hybridization, the antagonistic characters, brachytic internodes and long mesocotyls. In fact, so general is the extension of the brachytic nature of the internodes throughout brachytic plants that it is reflected in the homologous parts of the terminal panicle, as is shown by the reduced length of the branching space.

The first generation seedlings showed mesocotyls longer than the Hopi parent, but the Hopi strain used had been reduced much in vigor through continuous inbreeding.

The plants of the first generation were extremely unpromising, but several self-pollinated ears were obtained. Seeds of these, representing the second generation, were grown in the dark, permitting the complete elongation of the mesocotyl. There was no evidence of Mendelian segregation in this charac-

[1] Collins, G. N. A Drought Resistant Adaptation of Hopi Maize, *Jour. Agri. Research.* Vol. 1, No. 4, Jan. 10, 1914.

[2] Kempton, J. H. Heritable Characters of Maize, III Brachytic culms, *Jour. of Heredity,* Vol. XI, No. 3, March, 1920.

ter, as is shown in Fig. 1. To make certain that brachytic segregates were being obtained, since brachytic plants can not be distinguished in the seedling stage, a series of seeds were planted in the field at the bottom of paper mailing tubes set in trenches to permit filling around the plants after the tubes had been removed. The mesocotyls of these plants were measured after their elongation was complete, and the trench filled, the plants being allowed to mature. Of twenty-five mature plants seventeen were of normal stature and eight brachytic. The length of the meso-

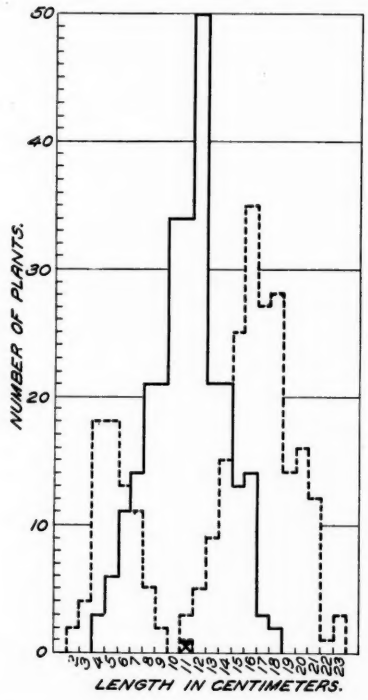


FIG. 1. Comparison of the nature of inheritance of internode length and mesocotyl length. These organs have been considered homologous, one being above, the other below ground. Polygon enclosed in solid line shows distribution of plants with respect to length of mesocotyl in a brachytic-Hopi hybrid (F_2). Polygons enclosed in dotted lines show distribution of plants with respect to length of longest internode in a brachytic-Boone hybrid (F_2). The small polygon at left represents the brachytic segregates, that at right the normal plants. The square marked X represents a plant classed as brachytic. The polygons are drawn on a basis of 265 individuals; the number of plants in the brachytic-Boone hybrid, while the number of plants in the brachytic-Hopi hybrid was 165.

cotyl varied from 10 to 15 cm in the normal plants with a mean length of 12.1 ± .22, while in the brachytic plants the mesocotyls ranged in length from 10 to 14 cm with a mean length of 11.7 ± .44. It is thus evident that there is no tendency toward a shortening of the mesocotyl, corresponding with the reduction in length of the internodes, of brachytic plants. The very different mode of inheritance of these characters is shown strikingly in Fig. 1, in which the distribution of the plants of the brachytic-Hopi hybrid with respect to mesocotyl length is compared with the distribution for length of internode in a brachytic-Boone hybrid.

It is apparent from this hybrid between brachytic and Hopi that no obstacle of inheritance prevents the combination of long mesocotyl with brachytic internodes, though the particular hybrid studied was unpromising from other standpoints. The failure of the mesocotyl to behave in inheritance in a similar manner to that of the internodes suggests the possibility that this organ is in reality an elongated node as held by Van Tieghem[3] and supported by the fact that roots may arise at any point on its surface.

J. H. KEMPTON

BUREAU OF PLANT INDUSTRY

CHELYS AND THE PHYLOGENY OF THE TURTLES

IN a recent paper, Hay[1] has brought forth some evidence which at first sight would seem to have considerable bearing on the phylogeny of the Testudinata. Perhaps the most disputed question in the phylogeny of the turtles centers about the relationship of the leathery turtle *Dermochelys*. Some investigators have considered this genus closely allied to the sea turtles, Cheloniidae, while others, such as Hay, would place the leathery turtle in a sub-order by itself, and group all the other recent Testudinata together under another sub-order.

Hay believes that considerable support is given to the latter arrangement by his discovery that the South American Matamata—*Chelys fimbriata*—sometimes possesses a series of irregular bony splinters overlying the carapace and covering parts of

[3] Van Tieghem, Philippe, Observations anatomiques sur le cotylédon des graminées. *Am. Sci. Nat. Bot.*, S. 5, T. 15, pp. 236–276. 1872.

[1] Hay, O. P., 1922, *Journ. Morph.* 36, pp. 421–441; pls. 1–2.

the plastron. Hay has examined the shells of six adult specimens of this species and in five of them has found some indication of these splinters. Three of these five shells are in the collections of the American Museum of Natural History and have attracted my attention.

Hay has postulated that the primordial turtle armature consisted of three layers of bone above the viscera, namely, (1) the ribs, (2) the carapace and (3) a set of bony nodules. Hay compared the series of bony splinters overlying the carapace in five of the specimens of *Chelys* which he examined to the bony nodules or outer bony layer of this primordial but purely hypothetical turtle. According to Hay, most existing turtles possess bony layers 1 and 2; the leathery turtle 1 and 3. *Chelys,* he believed, retained all three layers. A few fossil turtles, according to Hay, possessed some remnants of the outer layer of bone in their so-called epithecals.

It should be noted that all but one of the five specimens of *Chelys fimbriata* found by Hay to possess bony splinters, superimposed on the carapace and lying ventral to the plastron, were old captive specimens. The three specimens belonging to the American Museum, which Hay examined, had all been in captivity for some time. Only two specimens examined by Hay were preserved in the field, and one of these lacked the bony splinters. Captive specimens, especially those retained for any length of time in zoological parks, would be the especial objects of the attacks of parasites. In considering Hay's hypothesis it should also be noted that *Chelys fimbriata* is an excessively specialized Pleurodire and not a form in which one would expect to find ancestral features.

It occurred to me that the critical evidence for Hay's hypothesis should be furnished by the ontogeny of the shell, and the development of these bony splinters. Immature specimens of *Chelys fimbriata* are exceedingly rare in collections. Thanks to the courtesies of the Brooklyn Museum of Arts and Sciences, there is now in the collections of the American Museum an immature specimen captured at Caicarra on the Orinoco River, Venezuela, July, 1907, by Mr. George K. Cherrie. This specimen is apparently an individual of the second or third year. It is 203 mm in total length. The carapace is 124 x 91 mm; the plastron 102 x 72 mm. The greatest width of the head is 51 mm.

Instead of skeletonizing this specimen, I have cleared it by

means of a modification of the Schultze method. The entire animal was first stained delicately, with alizarin in order to differentiate any bony splinters, and to define clearly the sutures in the shell. On clearing it was found that the shell had not reached its full development. Three foramina were present along the median axis of the plastron. The largest of these foramina measured 13 x 10 mm. The carapace and plastron were not ankylosed together, a small space being present between them. The carapace exhibited a series of nine foramina along each side between marginals and costals. The bones of the shell were massive. The shell, although incomplete, was by no means embryonic. Practically all of the regions, which in the adult shell exhibited a series of bony splinters, were already well formed.

A careful examination of these regions under a strong transmitted light has failed to reveal any indication of the splinters. It is obvious that this specimen, like one of the adults examined by Dr. Hay, does not possess them. One may argue, of course, that in my specimen, although 203 mm in length, the splinters have not yet developed. Still, one would expect that, if these splinters have such a great phylogenetic significance, they would at least be represented by cartilaginous or fibrous anlagen. It is, perhaps, unwise to draw any general conclusion from a single observation. Nevertheless, as Dr. Hay's hypothesis is based upon such a limited series of specimens, it seems to me that the evidence offered by my specimen is significant. Hay's hypothesis should not be accepted without additional material.

In conclusion, it may be said that the ontogeny of the shell of *Chelys fimbriata* lends no support to the view that the splinters of bone, sometimes found on the shell of the adult, are remnants of a former layer of bone, homologous to the definitive shell of the leathery turtle. These splinters seem to be bony deposits formed over injuries received either during captivity or rarely in nature.

G. K. Noble

The American Museum of Natural History,
New York City

A NOTE ON THE THEORY OF SEX DETERMINATION

The recent important work of Bridges (1921, 1922) on triploid Drosophila has shown that sex is determined in this form by the relation between the X chromosomes and the sets of autosomes

present in an individual. Bridges has concluded from his data that the effective relation is the *ratio* between number of X chromosomes and the number of autosomes. This ratio is the same in completely diploid (2X + 2A, where A = one complete set of autosomes) and completely triploid (3X + 3A) individuals, and these individuals are females in Drosophila.

That the autosomes as well as the X chromosomes are concerned in the determination of sex has hitherto met with no such definite demonstration as that given by Bridges. In fact, the older chromosomal hypothesis ignored the autosomes and regarded maleness and femaleness as depending on the presence of one or two X chromosomes respectively (or vice versa in some cases). More recently, Goldschmidt has subscribed to the view that sex rests on the resultant of two opposing factors, but although he believes one of these to be located in the X chromosome, he regards the other as situated in the Y chromosome or else the cytoplasm of the egg.

In considering Bridges' hypothesis, it becomes evident at once that a haploid (X + A) Drosophila (which has not yet been discovered) must be a female. This introduces a difficulty which has sooner or later always been encountered in older hypotheses. It lies in our conception of chromosomal conditions in animals where males are haploid. In several groups (Rotifera, Thysanoptera, Aleyrodidae, Hymenoptera and Acaridae) there are forms in which it appears almost certain that females are diploid and males haploid. Regardless of how such a condition was brought about, it is commonly assumed that these types represent nothing but a modification of the ordinary type of sex determination. If Bridges' conclusions be accepted that view is no longer tenable, and we are forced to conclude that the sex-determining mechanism is of a different type altogether in the two cases. The purpose of the present note is to show that such a conclusion is not necessary, because the ratio view is not proven.

Bridges' results show clearly that the autosomes have, as a whole, a male-producing tendency and the X chromosomes a female-producing tendency. Let us arbitrarily call maleness the plus and femaleness the minus direction; let us assign a numerical value of —6 to the X chromosome, and one of +2 to one set of autosomes (or A). It is then to be assumed that the effective relation is the *algebraic sum* of X and A, rather than their ratio, a procedure which will be familiar to those who have read

Goldschmidt's papers on sex determination in the gypsy moth.

The remarkable series of forms identified in Drosophila by Bridges, with the addition of the haploid form, will then work out as follows:

Name	Constitution	Algebraic Sum
super-male	X + 3A	0
male	X + 2A	−2
haploid	X + A	−4
intersex	2X + 3A	−6
diploid female	2X + 2A	−8
triploid female	3X + 3A	−12
super-female	3X + 2A	−14

If we suppose the threshold value for maleness to be at −5 and that for femaleness to be at −7, the result is consistent with the view that the haploid Drosophila may be male. The bee may thus have essentially the same type of sex determination as Drosophila. It is not important in this connection whether we suppose that the drone has a single X chromosome, or whether the material represented by the X chromosome in Drosophila is distributed over the autosomes in male Hymenoptera.

No special significance is to be attached to the numerical values assigned to X and A; and it seems highly improbable that their effect depends on so simple a mathematical function as that employed here. The important point is that the data at present available do not demonstrate that the ratio between the number of X's and the number of autosomes is the effective element in the situation.

FRANZ SCHRADER
A. H. STURTEVANT

BRYN MAWR COLLEGE AND
COLUMBIA UNIVERSITY

THE PARALLEL CHARACTERS "CROSSVEINLESS" AND "VERMILION" IN DROSOPHILA WILLISTONI

IT has been shown by Lancefield and Metz[1] that certain sex-linked characters in Drosophila willistoni resemble characters in Drosophila melanogaster, Drosophila virilis and Drosophila obscura, not only in appearance but in their linkage relations. Attention may be called particularly to the characters "scute"

[1] R. C. Lancefield and C. W. Metz, AMER. NAT., lvi: 211, 1922.

and "yellow," which are almost completely linked and which resemble the similarly linked characters of like names in the other species, with the exception of virilis. In virilis scute has not yet been found, but yellow is present. The relations of these and other "parallel"[2] characters in the respective species has suggested that homology may be involved. Such a view is strengthened by the additional "parallels" crossveinless and vermilion considered below.

Crossveinless in D. willistoni is characterized by the absence of both cross veins in the wings and by a slight swelling of the fifth and, to a lesser extent, of other veins at their apices. With the exception of the slight swelling of the veins this character appears to be a duplicate of the crossveinless in D. melanogaster[3] and in D. virilis.[4] In D. obscura crossveinless has not yet been found.

Vermilion in D. willistoni has vermilion colored eyes. It also has whitish instead of yellowish ocelli. In both of these respects it resembles the sex-linked vermilion in D. melanogaster,[5] D. virilis[6] and D. obscura.[7]

The sex-chromosome "maps" representing the linkage relations of sex-linked characters in these species are given in the accompanying figure. Symbols are included only for the characters under discussion; others are indicated merely by cross lines marking the loci. These maps are arranged so that the locus of yellow, which is common to all, comes on a common line. This is used as the zero point in designating map distances.

In D. willistoni the amount of crossing over between scute and yellow is negligible; only one certain case has been found. This one, however, was such as to indicate that the locus of scute is above that of yellow. Yellow and crossveinless have given a crossover value of 2.1 per cent. on the basis of 1,435 flies, and crossveinless and vermilion have given a value of 0.3 per cent. on the basis of 1,351 flies. Tests involving the genes for scute,

[2] The term "parallel" is used to designate mutant characters similar in appearance and (usually) in linkage relations, in different species where homology can not be proved by crossing.

[3] Bridges, C. B., *Proc. Nat. Acad. Sci.*, 6: 660, 1920.

[4] Weinstein, A., *ibid.*, 6: 625, 1920.

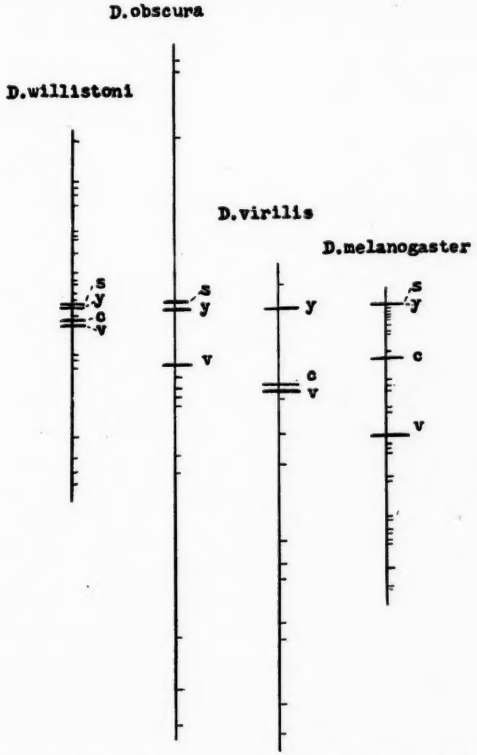
[5] Morgan and Bridges, *Carneg. Inst. Wash.*, Pub. 237, p. 27, 1916.

[6] Metz, Moses and Mason, *ibid.*, Pub. 328.

[7] D. E. Lancefield, *Genetics*, 7: 335, 1922.

yellow and crossveinless in one chromosome and vermilion in the other gave the following crossover classes among 891 flies: crossveinless 8, scute yellow vermilion 6, "wild type" 3. The latter appeared singly in three different bottles, making it practically certain that they represent crossovers and are not due to contamination. The results indicate that the order of the genes is scute yellow crossveinless vermilion, which agrees with the order in the other species so far as known.

When the accompanying maps are compared they reveal three features which require consideration here. In the first place the



series of loci under consideration falls near the end of the maps in two cases (melanogaster and virilis), but near the middle in the other two. This is believed to bear a significant relation to the fact that in the two former species the X-chromosomes are short and rod-like, while in the latter they are about twice as

long and are V-shaped.[8] Such a correlation between chromosome proportions and map proportions led to the suggestion[9] that the rod-like X's of melanogaster and virilis may possibly correspond to one arm of the V-shaped X-chromosome in willistoni and obscura. The evidence as a whole is still in accord with this view.

A second feature revealed by the maps is that although the serial order of the loci considered here is the same in all four cases,[10] the map distances involved differ considerably. In willistoni the distance from scute to vermilion is approximately 2.5 units, in obscura it is about 15 units, in virilis about 25 units and in melanogaster about 33 units. In all but the last case, however, these differences are associated with differences in total map lengths which indicate general differences in frequency of crossing over in the X-chromosomes. For instance, crossing over in the X-chromosome of obscura appears to be more than twice as frequent as in the willistoni X. Likewise crossing over appears to occur more frequently in the virilis X than in the melanogaster X. When the *relative* positions on the maps are considered the agreement is closer.

But there is one conspicuous exception, and this brings out the third feature requiring consideration. In willistoni and virilis crossveinless and vermilion are very closely linked. In melanogaster, on the other hand, the locus of vermilion falls at a point on the map nearly 20 units below that of crossveinless, and between the two are several other identified loci. It seems necessary to conclude in this case either that one of the two characters is not homologous to those in the other species, or else that a rearrangement of genes is involved. The evidence (which will be given in detail elsewhere) at present favors the latter view.

Only a portion of the known sex-linked "parallels" are included above; others, particularly singed and forked, might be added to the series, but a complete discussion is not intended in this brief note.

CHARLES W. METZ
RUTH M. FERRY

DEPARTMENT OF GENETICS,
CARNEGIE INSTITUTION OF WASHINGTON

[8] Metz, C. W., AMER. NAT., 1:587, 1916.

[9] See notes 1 and 6 for references.

[10] Scute and yellow in melanogaster appear to be completely linked; hence their relative positions are not known.